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VI. *A Minute Analysis (Experimental) of the Various Movements produced by stimulating in the Monkey different Regions of the Cortical Centre for the Upper Limb, as defined by Professor* FERRIER.

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[PLATE 7.]

THE following research was undertaken as a necessary preface to an investigation, which we are at present engaged upon, into the localisation of motor function in the cervical enlargement of the spinal cord.

Briefly speaking, the experiments from which the following conclusions have been drawn consisted in an elaborate examination of the movements elicited by stimulating with the interrupted induced current every part of the motor cortex in the Monkey, in which the upper limb is primarily represented, as first described by Professor FERRIER.

Before entering, however, on a detailed description of the present research, it will be necessary to discuss shortly the anatomical features of the parts of the cortex concerned.

Anatomy.—A glance at the accompanying diagram of the external or convex surface of the left cerebral hemisphere of the Macacque Monkey shows that FERRIER'S motor region is bounded inferiorly by the fissure of SYLVIUS, posteriorly by the intra-parietal sulcus, superiorly by the margin of the hemisphere, and anteriorly by a narrow strip of grey matter* in front of the vertical limb of the præcentral sulcus, and also by that sulcus itself. The central point of this area is the middle third of the ascending frontal convolution, and in this portion of the cortex and around it we have the cortical "centre" for the movements of the opposite upper limb.

Before enumerating the functions of this portion of the cortex it is incumbent upon us to draw attention to certain minute characteristics of the various sulci of this region, these being of great constancy, and therefore of primary importance in aiding exact localisation of function.

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* By this is meant portions of the bases of the frontal convolutions, the extent of which can be mapped out by electrical excitation.

Proceeding from the best known of these to those which hitherto have escaped especial notice, we will commence with the fissure of ROLANDO.

The *fissure of* ROLANDO, in all the species of Monkey on which we have experimented, runs outwards, forwards, and downwards, forming an angle of 50° to 55° with the mesial margin of the hemisphere. In its course it presents the following changes of shape, which in our experience are perfectly constant. Thus, for the uppermost quarter of its extent it presents a distinct, though slight, curve with the convexity forwards; in the next, *i.e.* the second quarter, it is slightly curved, with the convexity in the opposite direction, viz., posteriorly; and this curvature, concave anteriorly, runs down into the third quarter, in which part of its course the fissure presents a well-marked bend forwards. To this bend we would now direct especial attention, for it can be demonstrated to exist perfectly distinctly in Man and most Monkeys. Further, in the *Monkeys* we have examined, this bend is situated, as we have already said, in the third quarter of the fissure; its apex or central point is rounded, and is just above the horizontal level of the lower end of the intra-parietal sulcus, while, at the same time, it is well below the level of the highest point of the præcentral sulcus. From the apex of this bend the fissure of ROLANDO in its lowest fourth slopes almost vertically downwards (vertically signifying at right angles to the longitudinal fissure) towards the Sylvian fissure.

The *præcentral sulcus* is directed upwards and distinctly backwards from the base of the ascending frontal convolution, which it limits anteriorly. Just before it reaches the level of the central point of the fissure of ROLANDO, it bifurcates into two horizontal limbs; the anterior and longer runs forwards, being slightly curved with the concavity downwards; the posterior, on the other hand, is directed upwards as well as backwards, and is extremely short, very rarely exceeding 2 mm. in length. The main stem of the sulcus presents a double curve, the upper half having a slight convexity backwards, while the lower half is markedly curved forwards. In this way the ascending frontal convolution is most narrow opposite the posterior superior limb of this sulcus, while below it widens broadly.

Superior Frontal Sulcus.—In December, 1883, Professor SCHÄFER published in the 'Journal of Physiology' an account of the brain of a Macacque Monkey, which was shown by Professor FERRIER at the International Medical Congress in London, in which account he drew attention to the existence of a small, but definitely marked, sulcus on the upper portion of the frontal lobe, having an antero-posterior direction, and dividing into two parts the surface of the brain between the upper end of the præcentral sulcus and the mesial margin of the hemisphere. This small sulcus lies just behind the line of direction upwards of the vertical stem of the præcentral sulcus. Professor SCHÄFER provisionally named this sulcus x.

We venture to think that this small sulcus is nothing less than the representative of the posterior extremity of the superior frontal sulcus of Man, and that, therefore, the portion of brain above it must be looked upon as the first or superior frontal convolution, and that that part which lies between it and the top of the præcentral sulcus is certainly the second or middle frontal convolution. Finally, all that portion of the cortex which lies below the anterior horizontal limb of the præcentral sulcus must at present be regarded as of uncertain denomination, since, for several reasons which need not be detailed here, the upper third of it would appear to belong to the middle frontal convolution, while there can be little doubt that the lower two-thirds are homologous with the third or inferior frontal convolution of Man. We will now return to the consideration of the evidence on which we ground the opinion that x is really the representative of the posterior extremity of the superior frontal sulcus in Man. This evidence we will consider under the following headings :—

1. Morphological significance as an important sulcus.
2. Functional significance as an important sulcus.
3. Anatomical form and direction.
4. Value as a determinant of localisation of function.

1. *Morphological Significance.*—We have already stated that Professor SCHÄFER had previously observed the constancy of this small sulcus, which opinion is fully confirmed by our experience. He has further shown on a transverse section that it was marked by a distinct folding in of grey matter—the sure indication of an important sulcus.

2. *Functional Significance.*—We have found that if electrodes are applied to the sulcus itself no movement follows, whereas, if they be just shifted to either border, the characteristic effects about to be described are obtained. Here we have a functional proof that this sulcus, although small, definitely divides two portions of the motor cortex. These portions, we shall see directly, have a different function.

3. *Anatomical Form and Direction.*—With one exception, we have found that the most constant direction of this sulcus is antero-posterior, though frequently it is slightly oblique. The exception referred to was found in a pig-tailed Monkey (*Macacus nemestrinus*), in which specimen the sulcus was almost vertical, and consequently parallel, to the fissure of ROLANDO. Now we would submit that we have here faithful imitations of the varieties of form presented by the superior frontal sulcus in Man. For, as is well known, that sulcus is most frequently a more or less straight antero-posteriorly directed line, while sometimes, though more rarely, it resembles a miniature præcentral sulcus in possessing a vertical stem parallel to the fissure of ROLANDO, from the middle of which there runs forwards an antero-posterior limb. If, therefore, we regard this sulcus, x, as the posterior extremity of the superior frontal sulcus, its variations in form will be most easily understood. Finally, we would observe that the superior frontal sulcus in Man commences posteriorly, well behind the line of the præcentral sulcus, directed vertically upwards ; in fact, it begins posteriorly in the middle of the ascending frontal convolution. It is just this first part of the superior frontal sulcus which, lying over the anterior half of the breadth of the ascending frontal convolution, forms the sulcus, x, of the Monkey's brain.

4. *Value as a Determinant of Localisation of Function.*—We do not intend here to dwell on this point, because its full importance will be seen in the subsequent description of our experimental results obtained by stimulation, but we will anticipate so far as to say that this sulcus enjoys the distinction of separating the seat of the primary representation of the upper limb from that of the lower, a distinction which, it need hardly be added, is of the first importance.

Thus we have been led to designate this sulcus, x, by the more definite term of superior frontal sulcus, and we trust that the above evidence will be accepted as tending to establish this position.

The Intra-parietal Sulcus.—There is one variation in the form of this sulcus which we will notice, not merely because, so far as we know, it has not been described before, but also because it alters slightly the localisation of certain movements of the digits. This variation simply consists in a bending horizontally forwards of the lower end of the sulcus towards the fissure of ROLANDO, from which, in extreme cases, it is sometimes separated by only 3 mm. of surface of grey matter. This is particularly marked in the pig-tailed Monkey (*Macacus nemestrinus*). We shall refer to this point further.

Ascending Parietal Convolution.—We would draw attention to the fact that the upper end of this convolution—in other words, that part which represents in Man the parietal lobule—is invariably subdivided vertically by a subordinate sulcus, which is situated at the junction of the anterior and middle thirds of the convolution and runs down parallel to the fissure of ROLANDO. The lower end of this subordinate sulcus extends most frequently to the level of x, the upper end always being separated from the margin of the hemisphere by a few millimetres of cortex.

With the foregoing observations we conclude the anatomical description of the part under consideration.

PREVIOUS RESEARCHES IN THE SAME DIRECTION.

We will now describe the results obtained by Professor FERRIER on stimulating the same region, quoting verbatim from his 'Functions of the Brain,' 1st edition, 1876.

From the account there given we have drawn up the following Table, showing the relation between his nomenclature of centres stimulated and ours, and in the third column the results he obtained.

We find, however, that the area of cortex in which the upper limb is represented extends a little further towards the fissure of SYLVIUS than he has indicated; it is difficult also to make out the exact position of our centres 2 and 2′ in relation to his, but perhaps we may include them in his centre 6.

With these trifling differences, it will be seen that the broad facts in our account are practically identical with his, all minuteness of detail contained in the following pages being of course superadded by us.

TABLE 1.

FERRIER'S Centre.	Authors' Centre.	FERRIER'S Result.
3	12, 1′	Movements of the tail, generally associated with complex movements of thigh, leg, and foot, with adapted movements of the trunk by which the foot is drawn to the middle line of the body, as when the animal grasps with its foot or scratches its chest and abdomen.
4	1 9 (?) 11	Retraction, with adduction of opposite arm, palm of hand being directed backwards. This action . . . is such as may be ascribed to the latissimus dorsi.
6	3 3′ 4 4′	Supination, flexion of forearm by which the hand is raised to the face.
a *b* *c* *d*	7 7′ 8 behind 8′	Individual and combined movements of the fingers and wrist, ending in clenching the fist. Centres for the extensors and flexors of individual digits could not be differentiated, but the prehensile movements of the opposite hand are evidently centralised here.

We will now proceed to describe our method of experimentation, the results in full detail, and the generalisations which can be deduced therefrom.

Method of Experimentation.—The animal being thoroughly anæsthetised with ether, the left cortex was exposed *lege artis*, and the dura mater raised. A careful drawing was then made of the arrangement of the sulci, upon which was represented the position of the various points stimulated. The cortex, after being carefully dried to prevent diffusion of the current, was excited as follows. The apparatus employed was one DANIELL cell and an ordinary DU BOIS-REYMOND coil, but no attempt was made to equalise the make-and-break shock by means of a HELMHOLTZ wire. The electrodes were the ordinary platinum pattern, and were 2 mm. apart. The coil consisted of a primary bobbin wound round an iron core, with secondary bobbin sliding on a sledge over it, the distance between them being registered in centimetres, so that the strongest current would be at zero when the secondary coil completely covered the primary one. The primary current was interrupted by means of an ordinary NEEF'S hammer, and the secondary currents with this arrangement were of a strength sufficient to produce the sensation of slight pricking on the human tongue when the secondary coil was at 8, *i.e.*, 8 cm. from the primary. This very weak secondary current* was always employed so as to obviate the fallacy of diffusion. That this object was attained was obvious, for, if a certain movement was always obtained at one place, shifting the position of the electrodes for even one millimetre was sufficient to produce a totally different result.

* This was the weakest current which would produce a contraction in the muscles.

Since in all the brains we have experimented upon the positions of the principal sulci were perfectly constant, we regarded them as definite landmarks by which we could accurately ascertain in different brains the position of each centre.

Thus, commencing above in the ascending frontal convolution, we took as our first landmark the sulcus x, and in the horizontal line behind it we placed our two first centres, 1 and 1′ (these to be explained directly, see fig. 1), and then placed opposite the level of the upper end of the præcentral sulcus the centres 3, 3′. Dividing the interval between these points (which in the average brain of the animals we employed, *i.e.*, nine out of the ten experiments, was 1 cm. in length) into two equal parts, we designated the point of division by the ciphers 2 and 2′. Below 3 and 3′ we placed 4, 4′ and 5, 5′ at distances equal to that between 2, 2′ and 3, 3′.

(The distance between the electrodes was 2 millimetres, and they were applied parallel to the longitudinal fissure at the points designated by the figures described above. These points or centres were about 4 mm. apart. Thus a considerable interval was left between the centres, which we explored in the same way, but we have not deemed it necessary to give the results of exciting the cortex at these intervals, since in every case they simply corroborated the effects obtained by stimulating the parts bounding them.)

We further found that the ascending frontal and middle-frontal gyri were so broad as to necessitate a vertical subdivision. To meet this contingency, we employ the plain figures for the centres of the posterior half, and figures dashed thus, 1′, for the anterior half; both, of course, being on the same horizontal level.

On reference to Table 3 it will be seen that, with the exception of the fingers and thumb, the absolute number of times that any movement is produced is much less in the ascending parietal than the ascending frontal convolutions, and further that the representation of even the thumb and index decreases as the gyrus is explored from below upwards.

From our experiments it appears to us that the ascending parietal convolution has less claim than the ascending frontal to be considered as an area of extensive representation of movement. We have been so impressed with the importance of deciding this fact that we have usually explored the former gyrus with the current directly after the skull has been removed, and subsequently repeated our examination of it at various intervals during the experiment, so as to eliminate any error in the direction of loss of excitability of the cortex of this gyrus.

We would call attention to the extraordinary degree of symmetry which exists in all the Monkeys on which we have experimented, and also that this is not merely morphological, but also physiological. Although this is a matter of great interest, we cannot enter into it in further detail.

Before giving the detailed results of our work, we would lay down the following axioms founded on our experiments.

Axiom 1.—Viewing as a whole the "motor area" of the cerebral cortex for the upper limb, as defined by Professor Ferrier, we find that the regions for the action of the larger joints are situated at the upper part of that area, close to the middle line, while those for the smaller and more differentiated movements lie peripherally at the lower part of the area.

Axiom 2.—As a general rule, *extension* of all the joints, particularly of the wrist and elbow, is the most characteristic movement of the upper part of Ferrier's arm centre; while *flexion* is equally characteristic of the movements obtained by stimulating the lower part. Finally, between these two regions there is a small portion where alternate flexion and extension predominate, a condition to which we have given the name of *confusion*.*

We shall now proceed to give by means of tables the details of the experiments upon which the foregoing axioms are based.

In the following Table 2 we give general conclusions respecting the different movements of each joint obtained by stimulating the upper and lower half of the above-mentioned area.

Table 2.

Upper part of Area.	Lower part of Area.
Shoulder.—**Advancing.**	**Adduction** (nil in lower $\frac{1}{3}$).
Elbow.—**Extension** (uppermost $\frac{1}{5}$), Confusion (second $\frac{1}{5}$).	**Flexion** (remaining $\frac{3}{5}$).
Wrist.—(1) **Pronation** (upper $\frac{1}{3}$).	**Supination** (lower $\frac{2}{3}$).
,, (2) **Extension.**	**Extension** (flexion at end of action).
Posterior part of Area.	*Anterior part of Area.*
Digits.—**Flexion.**	**Extension.**
Thumb.—**Flexion** (nil in upper $\frac{1}{5}$).	**Flexion-Extension.**

Expansion of the foregoing Table (compare Table 2).

Shoulder.—In the above Table it will be noticed that rotation of the shoulder does not appear; this movement, though frequently observed, is but one of association. Rotation out occurs as the result of stimulating the lower three-fourths of the area, at least of that part which lies in front of the fissure of Rolando. In almost every case this rotation outwards was accompanied by flexion of the shoulder, so that the elbow was brought forward as well as rotated outwards.

Pure abduction was practically never seen by us, but it entered into the composition of the advancing movement, which we have shown to be characteristic of the upper fourth of the area. It will thus be seen that the movement of the shoulder, which we have called advancing of the arm, is neither pure flexion nor pure abduction, but a combination of these two.

Adduction is strongly characteristic of the movement of the shoulder in the lower half of the area. Indeed, a glance at Table 3 will show that it is almost the only movement in the lower third of the area, in which portion of the cortex, too, the joint is very feebly represented, movement of it only being met with once in ten times on stimulating the centre 5′. (See fig. 2 and Table 3.)

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* Here both flexors and extensors are contracting at the same time, and consequently the joint is usually fixed in a median position, each group of muscles alternately dragging it in opposite directions.

Adduction is the characteristic movement of the shoulder "centres" in the ascending parietal gyrus. Retraction (*i.e.*, extension with rotation out and some adduction) is especially represented in the anterior half of the upper third of the ascending parietal gyrus in the centres marked 9 and 11. (See Table 3.)

Circumduction was never seen.

Elbow.—We need only draw especial attention to the remarkably exact manner in which representation of extension of the elbow is limited to the upper fifth of the area experimented on, while flexion is equally the function of the lower three-fifths; and to the existence of a very important zone of cortex, where the phenomenon of confusion is represented, this forming a border-land between the regions of extension and flexion. The explanation of this zone of confusion is easy, since the representation of the elbow—the movements of which occur in only one plane—admits necessarily of closely limited localisation. (See Table 3 and fig. 3.)

Wrist.—In tabulating the movements of this joint, it was obviously necessary to separate its two distinct functions, viz., pronation and supination, on the one hand, and flexion and extension on the other. We will first discuss the latter function, as by far the more important. On Table 3 it is seen how extremely constant is the movement of extension, and a moment's consideration will show that it is of fundamental importance, for it is clear that the delicate movements of the fingers could not possibly be performed with any degree of accuracy and force unless the wrist be previously fixed in moderate extension, and consideration of this fact also explains why the wrist is especially provided with powerful extensor muscles which act with considerable independence. (See fig. 4.)

In returning to the first-mentioned movements of the wrist, viz., pronation and supination, we have only to add that, as might be expected, supination is most marked in the lower two-thirds of the area, since it is here that we have also flexion of the elbow, *i.e.*, bicipital action. The converse equally holds, viz., that pronation is associated with extension of the elbow. This association is clearly the outcome of the two great classes of action in animal life, viz., that of defence and that of feeding. The former of these is a coarse violent movement, and is naturally associated in the upper part of the region with the centres for the large trunk and leg muscles, while the latter, more delicate, is represented near to the centres for the face and mouth.* (See Table 2.)

Digits.—The representation of the fingers must be considered apart from that of the thumb, the movements of which are the most highly specialized in the limb.

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* Similar ideas have been previously suggested by Dr. LAUDER BRUNTON, F.R.S. See 'Brain,' vol. 4, p. 431.

We would first draw attention (see fig. 5) to the fact that the movement of simple extension is alone represented in the posterior extremity of the middle frontal convolution (according to our view), viz., at centres 12, 13, 12′, and 13′ (see Table 3 and fig. 5). It will be observed on Table 3 that in three instances we noted interosseal flexion in this region. Discussion of the relation between interosseal flexion and extension of the digits we shall enter into further on.

As regards the movement of flexion, we find that it is represented over the whole of the area which has been the subject of our investigations, with the exception of the centres above mentioned, viz., 12, 13, 12′, and 13′. We have now to draw attention to some extremely important considerations concerning the relative representation of the movements of flexion and extension. We have just seen that pure extension was limited to certain centres; we have now to add that we have only seen pure flexion at centres 1, 1′, 4, and 4′. We are not inclined to lay much stress on this limitation of the representation of the movements of pure flexion and extension, but we note the foregoing facts for the purpose of recording them.

We will now consider what appears to us the much more important co-operation of these two movements of flexion and extension of the digits. On this point we have obtained the exceedingly definite result that both movements are represented in the middle $\frac{1}{3}$ of the ascending frontal and parietal convolutions, and that, while in the ascending frontal convolution extension precedes flexion, in the ascending parietal convolution this order is reversed, and so extension follows flexion. In view of the fact that pure extension is only represented in 12, 12′, 13, and 13′, *i.e.*, in those centres which are immediately in front of the middle $\frac{1}{3}$ of the ascending frontal convolution, we readily understand how it comes about that in the ascending frontal extension *precedes* flexion, whereas behind the fissure of Rolando it *follows* flexion. We have observed interosseal flexion to precede long flexion in three cases, and only in the centres 8′, 2, 2′, 12, and 3. It is obviously possible that this interosseal flexion of the digits, consisting of flexion of the metacarpo-phalangeal joints and extension of the phalangeal joints, should co-exist in perfect harmony with long extension of the digits. It must not be understood that in all the remaining cases interosseal extension of the phalanges leads the way for the action of the long extensors; indeed, in many instances it appeared to us that preliminary extension of the digits was so sharp and complete as to be explained only by rapid and perfect action of the long muscles. We must add, however, that, although this preliminary extension of the fingers was extremely well marked, it was of very brief duration, whereas the subsequent flexion was very powerful, and was maintained as long as the electrodes were applied to the cortex.

Although we have thus written at some length on the relation between flexion and extension of the digits, we do not consider that the results were sufficiently absolute to permit of our speaking dogmatically, and we hope that further research will ultimately solve this problem.

Thumb.—The limitation of the representation of the thumb in the cortex (see fig. 6) is a matter of great interest, considering that it is the most highly differentiated member of the body. The representation is limited to the ascending frontal and parietal convolutions. No movement could be elicited by stimulating the centres 1, 1′, 5, and 11; to these we must add 2 and 2′, as being centres in which the thumb was only exceptionally represented, *i.e.*, in one-third of the total number of cases for 2, and one-fifth for 2′. It is interesting to observe that the thumb obeys the same general rules respecting the relations of the movements of flexion and extension as do the digits; thus extension *precedes* flexion in the ascending frontal and *follows* flexion in the ascending parietal. The movement of opposition, which is, of course, the most highly differentiated one, was only obtained on stimulating the lowest part of the thumb area, viz., the centres 7 and 5′; this is in perfect harmony with the general plan of representation, as we have found it to exist in the outer convex surface of the cortex. (See Axioms 1 and 2.)

We may here refer to the fact that in 5′, in the ascending frontal gyrus, we obtained in two cases abduction of the thumb, whereas adduction was present in two cases in centre 7 in the ascending parietal; this is a further illustration of the fact that extension is represented in the ascending frontal, and flexion in the ascending parietal convolutions.

Before leaving the consideration of the representation of the thumb, we would briefly draw attention to the fact that the representation of the thumb extends lower down anteriorly, *i.e.*, just behind the præcentral sulcus, than that of any other part of the upper limb. Thus it is represented at centre 5′, but not in centre 5, &c. (See Table 3.)

We employ throughout our paper this expression—Primary Movement—in a very definite sense, namely, to express that movement which is represented above all others at one particular spot in the cortex. This use of the expression is in harmony with Dr. Hughlings Jackson's view, viz., that cerebral localisation is in the main a matter of degree of representation of several movements, and not the close limitation of any one. We were brought to the necessity of closely examining this point, not from the considerations of theories, but by observing with what remarkable constancy the various joints of the limb took up movement in series according to the part of the cortex stimulated, and how invariably one joint would commence the action when we adopted a method of excitation which we may call instantaneous or minimal stimulation.

Priority in the Order of Movements. (See fig. 7.)

We may now return with advantage to a detailed consideration of Axiom 1, viz., that the larger muscles are represented in the upper part of the motor area for the upper limb, while the smaller ones have their centres in the lower part of that area.

It seemed to us highly important, as bearing on this point, to note the order of movement of the different segments of the limb,—in fact, the "march," as it has been termed by Dr. HUGHLINGS JACKSON, of the nerve discharge,—since we consider that a complete series of observations of this kind would enable us to construct a definite scheme which would show at a glance where certain primary movements are really centralised.

By this we mean that we applied the electrodes to the cortex just long enough to evoke movement in one joint only, and then noted which moved first, and in what direction. This first movement we considered to be the primary or fundamental movement in the given portion of cortex stimulated. (The current employed in every case was only just adequate to produce such movement, and the secondary coil was usually 10 cm. distant from the primary coil.)

On fig. 8 is exhibited that joint in which primary movement occurs in each portion of the area.

In taking each joint separately, it is found that the shoulder presents priority of movement in the centres 1, 1′, 11 ; while the wrist is the first to move when we stimulate the centres 2, 2′, 12, 13, 3′. It is important to notice that the elbow does not present any absolute priority of movement over the other joints, for its only approach to priority is seen at centres 8, 8′, and 9, where it is associated with, and shares this action synchronously with, other joints, viz., the thumb and wrist. With regard to the fingers alone, the same thing is to be observed, viz., that they are not represented in primary movement in the cortex, and indeed are only associated once with a true primary movement, viz., in centre 12. Starting now with the series of joints moved as represented schematically in fig. 8, we will take up the order in which the other joints of the limb are secondarily moved.

Tabulating these joints in the order of centres stimulated, we have the following list :—

Ascend. Frontal Convolution. Centre.	Order of Joints moved.
1.	**Shoulder** $\left\{\begin{array}{l}\text{elbow,}\\ \text{wrist,}\\ \text{fingers.}\end{array}\right.$
1′.	**Shoulder**, elbow $\left\{\begin{array}{l}\text{wrist,}\\ \text{fingers.}\end{array}\right.$
2.	**Wrist,** fingers, elbow, shoulder.
2′.	**Wrist** $\left\{\begin{array}{l}\text{fingers}\\ \text{elbow}\end{array}\right\}$ shoulder.
3.	**Thumb,** fingers, wrist, elbow, shoulder.
3′.	**Wrist** $\left\{\begin{array}{l}\text{thumb}\\ \text{fingers}\end{array}\right\}$ elbow, shoulder.
4.	**Thumb,** wrist, fingers, elbow, shoulder (4).
4.′	**Thumb** $\left\{\begin{array}{l}\text{fingers}\\ \text{wrist}\end{array}\right\}$ elbow, shoulder (2).
5.′	**Thumb,** fingers, elbow $\left\{\begin{array}{l}\text{wrist (1),}\\ \text{shoulder (1).}\end{array}\right.$
Ascend. Parietal Convolution.	
11.	**Shoulder** $\left\{\begin{array}{l}\text{wrist}\\ \text{elbow}\end{array}\right\}$ fingers.
9.	$\left.\begin{array}{l}\textbf{Thumb}\\ \textbf{Elbow}\end{array}\right\}$ fingers, wrist, shoulder.
8′.	$\left\{\begin{array}{l}\textbf{thumb}\\ \textbf{wrist}\\ \textbf{elbow}\end{array}\right\}\left.\begin{array}{l}\text{shoulder}\\ \text{fingers}\end{array}\right\}$
8.	$\left\{\begin{array}{l}\textbf{thumb}\\ \textbf{elbow}\end{array}\right\}$ fingers, wrist.
7′.	**Thumb,** elbow, shoulder (1).
7.	**Thumb,** fingers, wrist, elbow (1).
Middle Frontal Convolution.	
12.	$\left\{\begin{array}{l}\textbf{Wrist}\\ \textbf{Fingers}\end{array}\right\}\left.\begin{array}{l}\text{elbow}\\ \text{shoulder}\end{array}\right\}$
13.	**Wrist**, fingers, elbow, shoulder.

The figures in parentheses show the greatest number of times out of a total of 10 in which a movement in the joint was produced.

As is shown in this Table, the sequence in the movement of the joints is fundamentally similar to that which had been arrived at from clinical observation by Dr. HUGHLINGS JACKSON in cases of epilepsy, in which he had recorded the "march" of the movements of the joints.

As all the facts which we have accumulated on the subject of the primary representation of movement of joints and the representation of secondary, &c., movements are collated in a very demonstrative manner in the accompanying figs. 7 and 8, a detailed description is hardly called for, but we cannot leave this pathologically very important subject without dwelling for a moment on some of the more salient features of our results.

We have already pointed out on page 163 why the shoulder, wrist, and thumb are the joints, *par excellence*, in which primary movement takes place.

We will now, therefore, discuss the march, *i.e.*, the order in which the movements of the various joints follow each other after the primary movement. The first and most fundamental fact concerning the successive invasion of the various joints has already been determined by Dr. HUGHLINGS JACKSON, viz., that when a movement emanating from the cortex, *e.g.*, of the upper limb, begins in the shoulder it proceeds downwards, involving successively the elbow, wrist, and fingers; and inversely, when it begins in the thumb and fingers, the "march" proceeds up the limb. We are here referring to movements presenting the characters of deliberate purpose, "voluntary" efforts, which also can be evoked by electric stimulation of the cortex, besides being exhibited in convulsive and epileptiform seizures. The observation of these movements as produced in our experiments has enabled us to form certain definite generalisations concerning the order of their march. Among these generalisations, the following appear to us to be the most important.

1. Movement of the upper limb, commencing with the shoulder, is not completed by a movement of the thumb; and, while this result is obtained at the extreme upper limit of the area, on the other hand, we have the exact converse at the lowest limit, viz., movement of the limb, commencing in the thumb, and ultimately involving the elbow, which is not completed by movement of the shoulder. In fig. 8 is shown diagrammatically the order of the march of movements occurring at each point in the area for the upper limb.

2. We wish next to point out the very remarkable constancy in the order of march in the centres 2, 2′, 13 (fig. 8). Here we are dealing with the very nucleus of the upper limb area, *i.e.*, that part of it in which the most frequent and most ordinary movement of the limb is represented, viz., preliminary fixation of wrist in extension, intended, as we think, for the purpose of permitting accurate movement of the digits; following this, flexion of the digits; next flexion of the elbow and subsequent adduction and rotation out of the shoulder, producing the complex movement which has been popularly styled the hand-to-mouth action, and which is unquestionably one of the most

important of the limb. The remarkable way in which this movement is represented in a nearly horizontal line on the cortex must not be overlooked.

Finally, fig. 8 illustrates most clearly how the mode of march is in harmony with the representation of primary movements in the various points in the area. Thus the movements consequential to the first movement obey the law we have already dwelt upon, viz., that the joints are represented from above down in the area, in the order of shoulder, elbow, wrist, digits, and thumb. The truth of this statement is rendered very evident when fig. 7 is compared with fig. 8.

To summarise briefly the facts contained in the foregoing pages, we consider :—

1. That sulcus x (SCHÄFER) corresponds to the superior frontal sulcus of Man.

2. That the muscles of the upper limb are progressively represented from above downwards, in the outer or convex surface of the hemisphere, in the order of their size and the movements of the joints: in the order of shoulder, elbow, wrist, finger, thumb.

3. That the joints are moved in the order of shoulder, elbow, wrist, and hand when the highest part of the area is stimulated, and in the converse order—thumb, fingers, wrist, elbow, shoulder—when the lowest part is excited, whilst between these extreme points the sequence of movement is commenced by a middle joint, *i.e.*, the elbow (incompletely), in the ascending parietal convolution, and the wrist to a very large extent in the ascending frontal.

4. That with regard to the quality of movements of the different joints represented in the cortex, the *shoulder* presents the following sequence from above down: advancing, abduction, rotation out, adduction; the *elbow:* extension, confusion, flexion; the *wrist:* extension, flexion, and pronation, confusion, supination. In the fingers and thumb the sequence is altered, and we have, broadly, extension anteriorly and flexion posteriorly. (For details refer to diagrams.)

5. That there is no *absolute* line of demarcation between the area of localisation in the cortex of one movement and that of another; each movement having a centre of maximum representation, this gradually shading off into the surrounding cortex.

TABLE 3.—*Résumé.* (Ten Experiments ; one incomplete.)

	Thumb.	*Fingers.*	*Wrist.*		*Elbow.*	*Shoulder.*
Ascending Frontal Gyrus.	1. Nil.	Flexion, 5.	Extension, 3.	Pronation, 4.	Extension-flex., 90°, 9.	Advancing abd., 10.
	1′. Nil.	Flexion, 7.	Extension, 3.	Pronation, 5.	Extension, 10.	Advancing abd., 9.
	2. ? Flexion-extension, 4.	Ext.-flexion, 10.	Extension, 3.	Pronation-Sup., 4 to 4.	Flexion-confusion, 5 to 5.	Rot. out. add. abd., 7.
	2′. Slight extension-flexion, 3.	Ext.-flexion, 9.	Extension, 7.	? Sup. 3.	Flexion-confnsion, 5 to 5.	Rot. out. add. abd., 8.
	3. Slight ext.-flex., 5 to 2.*	Ext.-flexion, 1 to 8.	Extension, 4.	Snpination, 5.	Flexion, 10.	Rot. out. add. abd., 8.
	3′. Ext.-flex., 2 to 1.	Ext.-flexion, 4 to 2.	Extension, 5.	Supination, 4.	Flexion, 5.	Rot. ont. add. abd., 6.
	4. Ext.-flex., 2 to 4.	Flexion, 5.	Ext.-flex., 3.	Sup.-pron., 5.	Flexion, 9	Add. rot. out., 5.
	4′. Ext.-flex., 3 to 5.	Flexion-ext., 8.	Extension, 2.	Sup.-pron., 5.	Flexion, 9.	Add. 4.
	5. Probably *nil.*	1 exception, same as 4′.				
	5′. Ext.-opp.-abd., 8.	Ext.-flexion, 4.	Extension, 1.	.. ..	Flexion, 2.	Add., 1.
Ascending Parietal Gyrus.	7. Flexion-add.-opp., 6.	Flexion-ext., 4.	Slight flexion, 1.	Slight sup., 1.	Flexion, 2.	Nil.
	7′. Slight flex.-ext., 2.	Inteross. flexion, 1.	.. ..	.. ..	Flexion, 1.	Rot. out., 1.
	8. Flexion-ext., 3 to 1.	Flexion-ext., 7.	.. ..	Sup.-pron., 2.	Flexion, 4.	Rot. out., 1.
	8′. Flexion-ext., 3.	Flexion-ext., 6.	Extension, 2.	Supination, 1.	Flexion, 3.	Abd. confusion, 1; add. retr., 1.
	9. Extension, 1.	Ext.-flexion, 3.	Extension, 2.	.. ..	Flex.-conf., 2.	Add., 2.
	11. Nil.	Flexion-ext., 2.	Extension-flex., 2.	Pronation, 1.	Conf.-flexion, 3.	Adduction with retraction (Lat. dors.), 4.
Middle Frontal Gyrus.	12. Nil.	Extension, 6; inteross. flex., 1.	Extension, 6.	Pronation, 1.	Confusion, 7.	Rot. out. abd., 5.
	12′. Nil.	Extension, 1; interosseal flex., 2.	.. ..	.. ..	Confusion, 2.	Rot. out., 1.
	13. Nil.	Extension, 2.	Extension, 3.	Supination, 1.	Flexion, 4; 90°, 2.	Rot. out. add., 2.
	13′. Nil.	Extension, 1.	.. ..	Supination, 1.	Flexion, 1; 90°, 2.	Rot. out. add., 2.

N.B.—The sequence of movement is indicated by the amount of underlining, thus:—The primary movement is denoted by one line, the secondary by two lines, and the third and fourth by three and four lines respectively.

Note.—The numbers *following* the record of each movement indicate the number of times that any action was obtained by stimulating the given centre. As before mentioned, we do not here give the results of stimulating the centres indicated by fractions, *i.e.*, the areas of cortex intervening between the above enumerated centres, because they simply corroborated the observation that the representation in one centre gradually merged into that of the next.

* Adduction in one case.

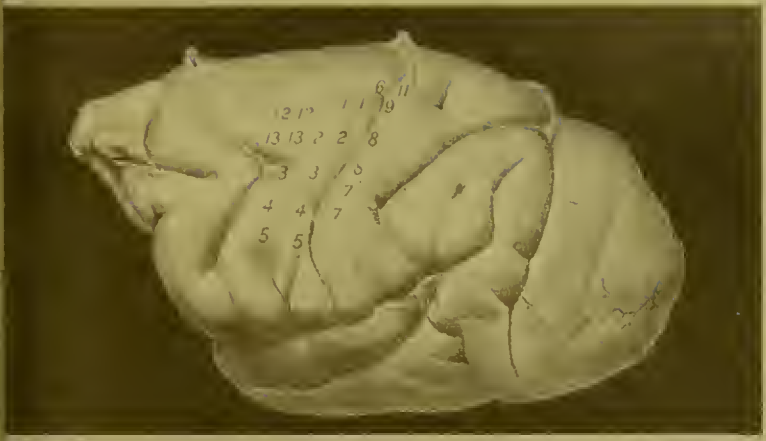


Fig 1

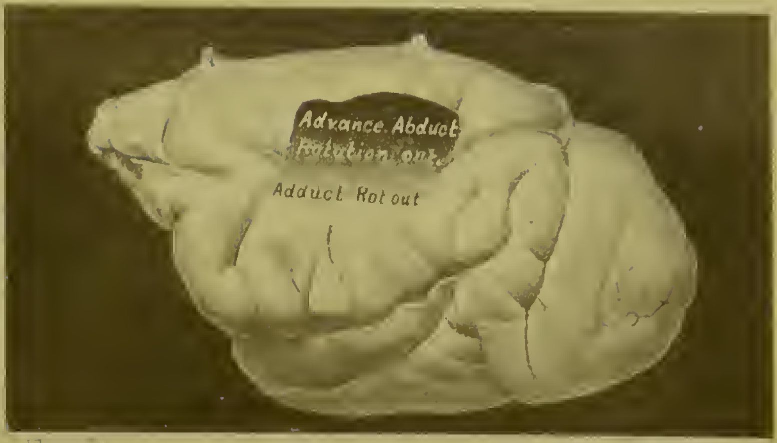
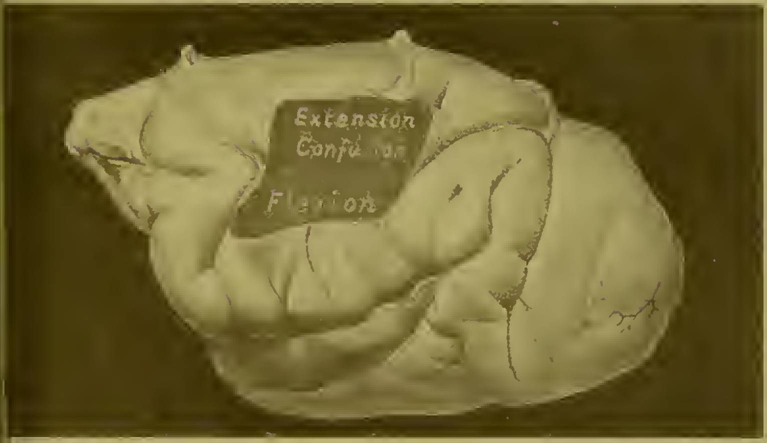


Fig 2



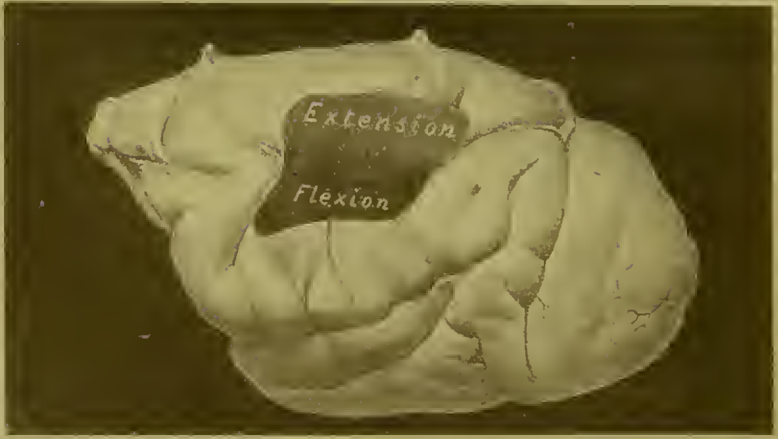
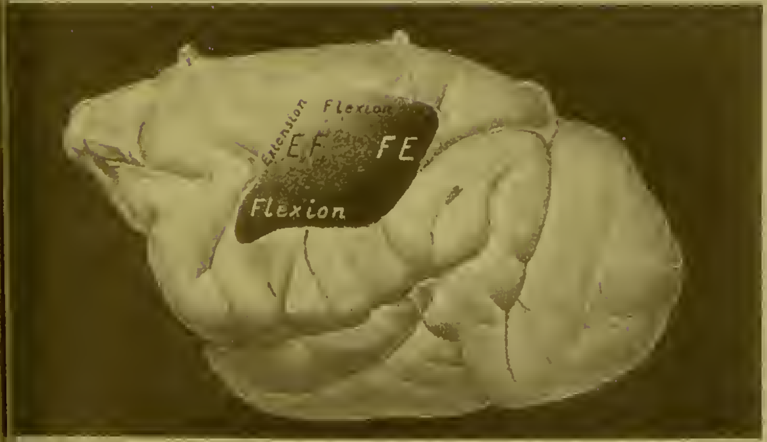


Fig 4



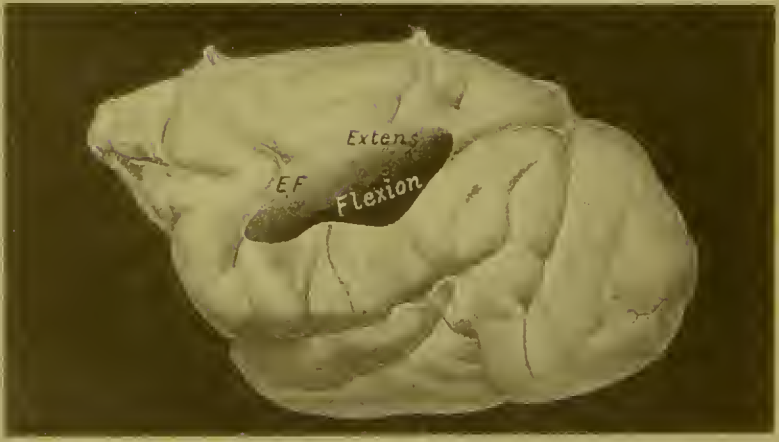
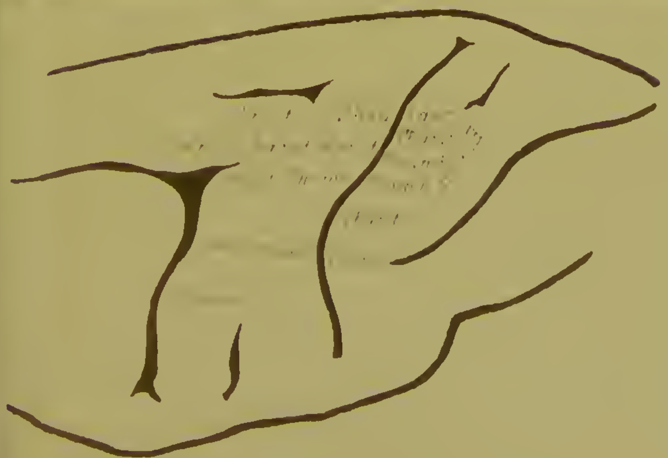
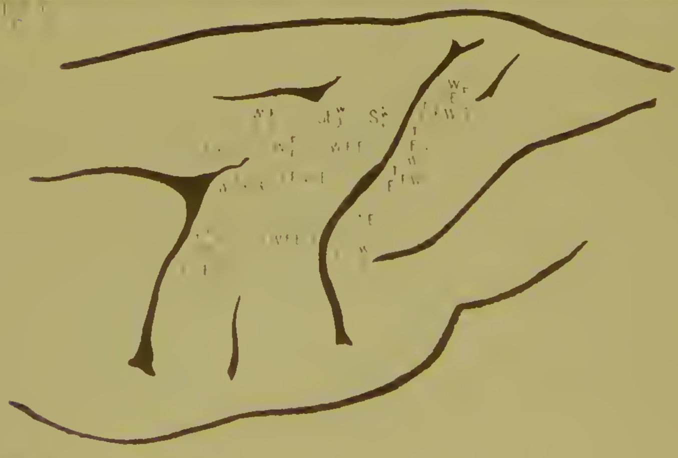


Fig 6





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IX. *A further Minute Analysis by Electric Stimulation of the so-called Motor Region of the Cortex Cerebri in the Monkey* (Macacus sinicus).*

By CHARLES E. BEEVOR, *M.D., F.R.C.P., and* VICTOR HORSLEY, *B.S., F.R.C.S., F.R.S.*
(*From the Laboratory of the Brown Institution.*)

Abstract received and read June 16,—Full paper received August 12, 1887.

[PLATES 40–42.]

INTRODUCTION.

IN a former paper published in the 'Philosophical Transactions,' B., vol. 178 (1887), pp. 153–167, a minute account was given by us of the effects produced by electrical stimulation of the so-called motor area in the cerebral cortex for the upper limb. In continuation of this work we have investigated in a similar manner the effects produced by stimulating the rest of the so-called motor region on the convexity of the cortex, with the exception of the lower parts of the ascending frontal and parietal convolutions. The parts examined in the present research comprise the posterior third of the frontal convolutions, the upper third of the ascending frontal convolution, the superior parietal lobule, and the posterior half of the ascending parietal convolution. The movements evoked by stimulating these areas were respectively those of the head and eyes to the opposite side, conjoined movement of both opposite limbs, movements of the lower limb, and movements of the upper limb. In order to avoid discrepancies in the arrangement of the cerebral sulci in different species, and so to obtain exact localisation of the effect produced, the same variety of Monkey was alone used, viz., *Macacus sinicus*. In all we have performed twenty-three experiments, the animal in each case having been narcotised with ether and killed before recovery from the anæsthetic.

PART I.—ANATOMY.

In the paper above referred to, a description was given of the position in the Monkey of the fissure of ROLANDO, the præcentral sulcus, and a small fissure above

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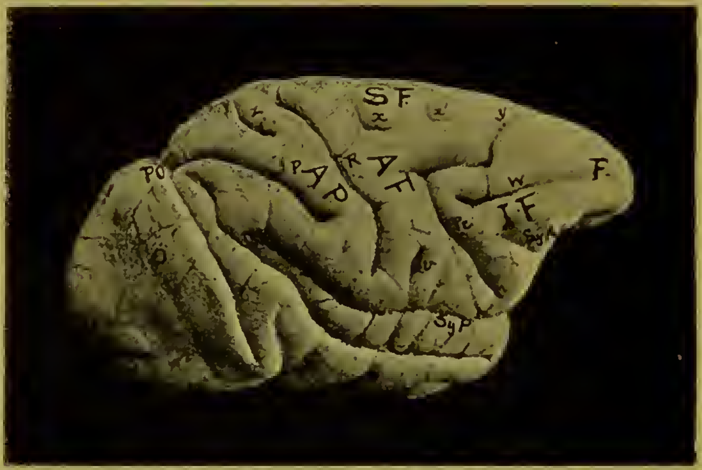
* The expenses of this research were defrayed by a grant from the British Medical Association.

this, called by Professor SCHÄFER "*x*." The excitable region investigated in the present paper is limited below, where it lies in front of the præcentral sulcus, by the horizontal level* of the lower end of that sulcus, the superior and anterior part being bounded above by the middle line, and in front by a sulcus which Professors HORSLEY and SCHÄFER provisionally named "*y*" (see fig. 1). Below, it is partially bounded by a sulcus which we have temporarily called "*w*." This sulcus, "*w*," runs horizontally from near the tip of the frontal lobe backwards to within a very short distance of the vertical limb of the præcentral sulcus, thus lying below and approximately parallel to the upper limb of the præcentral sulcus. The homology between this sulcus and corresponding parts of the human brain has not as yet been made out. The middle part of the region investigated in the present research is bounded above

Fig. 1.



Photograph of the external surface of the right half of the brain of a Monkey (*Macacus sinicus*).

Sulci	S*y*A.	Fissure of SYLVIUS, anterior limb.	
	S*y*P.	Fissure of SYLVIUS, posterior limb.	
	R.	Fissure of ROLANDO.	
	PO.	Parieto-occipital fissure.	
	IP.	Intra-parietal sulcus.	
	P*c*.	Præcentral sulcus.	
	v.		Sulci, so named.
	w.		
	x.		
	x′.	Supplementary to *x*, occasionally found.	
	y.		
	z.		

Convolutions or Gyri.	F.	Tip of frontal lobe.	SF.	Superior frontal.
	IF.	Inferior frontal.	AF.	Ascending frontal.
	AP.	Ascending parietal.	O.	Occipital lobe.

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* *I.e.*, a line parallel to, and a short distance above, the Sylvian fissure.

by the longitudinal fissure and below by the sulcus "x." The remaining part of this region, situated behind the fissure of Rolando, is bounded above by the longitudinal fissure, behind by the intraparietal sulcus, and below by the horizontal level of the lower end of that sulcus. The upper part of the ascending parietal convolution, or as it is also called the superior parietal lobule, is divided by a small sulcus which is usually vertical, and which has been designated "z" by Professors Horsley and Schäfer (see fig. 1).

(As we showed in our previous paper, we consider that the sulcus "x" separates the superior from the middle frontal convolution, and is consequently homologous with the superior frontal sulcus of Man.)

On looking at fig. 1 it will be seen that the portion of the cortex treated of in this paper partly surrounds the area in which the upper limb is chiefly represented—as described in our former paper—on two sides, viz., in front and above. These parts of the cortex in front and behind the area for the upper limb form the anterior and posterior limits respectively of the cortex which is excitable. The present research completes the investigation of the upper part of the excitable region of the outer convex surface of the hemisphere.

Topographical Determination of the Sulci.

The position of the sulci in different Monkeys of the same species and of about the same age varies considerably. These variations were noted in the following way:—the brain of each Monkey was exposed, and the part to be investigated was drawn the exact size, the distance of the sulci from each other and the size of the convolutions being measured by compasses; thus an accurate representation of each individual brain was recorded. As can be well seen by referring to figs. 1A and 1B, noteworthy variations in the outlines of the sulci were thus revealed.

Fig. 1A.

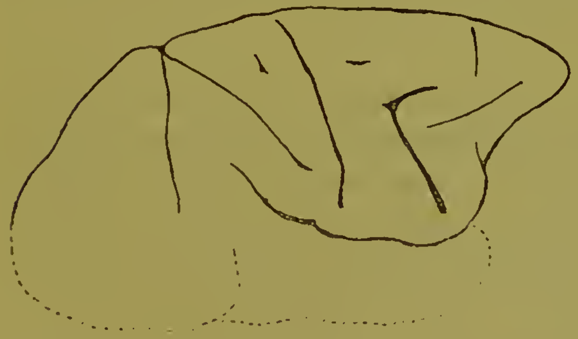
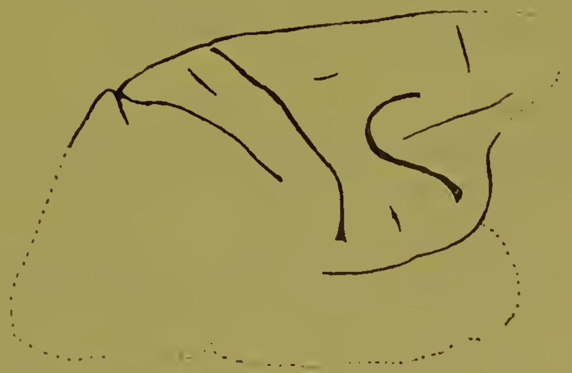


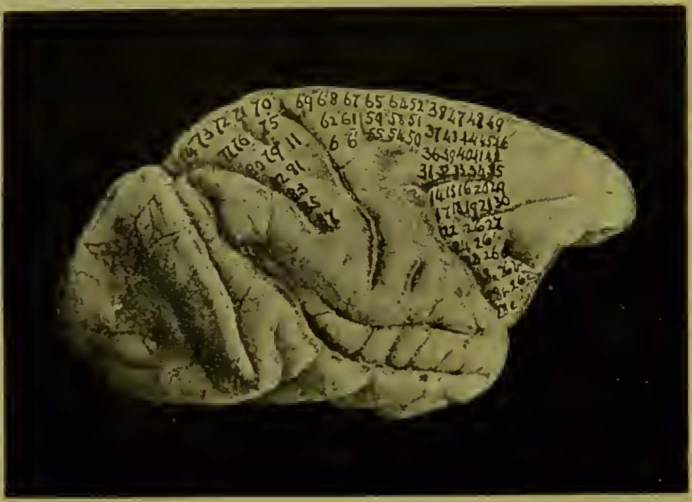
Fig. 1B.



PART II.—METHOD OF NOTATION OF THE VARIOUS POINTS STIMULATED.

Method of Experimentation.—We have, as before, divided up the area to be examined into centres* of 2 mm. square; but, although in our former research we investigated the contiguous borders as well as the middle point of these minute divisions, we thought it sufficient then to record only the latter half of these observations. In describing our present research we have thought it better to record the result obtained at every point stimulated. Consequently, in any given linear centimetre there will be five points of stimulation: that is to say, the electrodes being as before, 2 mm. apart, the middle of each centre will be 2 mm. distant from the middle point of an immediately contiguous one. The mere difference in size of the brain of some of the Monkeys investigated compelled us to slightly alter this arbitrary arrangement by suppressing a row of these centres where the approximation of the sulci reduced the surface area of the excitable cortex, so that there was only room for two in place of three rows of numbers. Moreover, occasionally we have been compelled to spread out the numbers, but the error of position so caused was never more than ·5 mm. As the method of notation of these small centres was quite arbitrary, and as numbers had to

Fig. 2.



This is a similar photograph to fig. 1, and shows the area of the cortex, which is the subject of this paper; the numbers denote the different individual points of stimulation, of which 74 are here given. Each number denotes a centre of the size of 2 sq. mm. Centres 35, 42, and 46 apparently pass anterior to the sulcus y (see fig. 1), but the deep shadow is caused by a large vein which happened to be present in this brain.

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* By the word centre, we mean each of the 2 mm. square divisions into which we have partitioned the region investigated. We reserve the term area to designate the total cortical surface in which movements of one part (*e.g.*, a limb) are wholly represented, *i.e.*, the upper limb area, the face area, etc.

be occasionally omitted owing to the inequalities and irregularities of a convex surface such as that of the brain, it has been impossible to maintain a perfect continuity in sequence of the numbers employed. (Reference to figs. 1 and 2.)

Method of Stimulation.—We have used as before the faradic current, employing such an one as would only just evoke a movement, and for the detection of the primary movement (see 'Phil. Trans.,' *l.c.*, p. 163) the method of momentary application of the stimulus. The sole change made in the apparatus has been the substitution of one litre bichromate of potash cell for the single DANIELL cell.

The parts of the cortex relegated to the representation of the various parts of the body observed to move on excitation of the different centres must now be described, in order to make clear the details of the subsequent analysis.

PART III.—THE TOPOGRAPHY OF THE REPRESENTATION OF THOSE PARTS OF THE BODY, OF WHICH MOVEMENTS WERE OBSERVED IN THE PRESENT RESEARCH.

(See fig. 3.)

(I.) *The Head and Eyes.*—The area of representation of the fundamentally important movement of turning the head and eyes to the opposite* side is a very extensive one, reaching from the longitudinal fissure above almost to the fissure of SYLVIUS below. It is limited in front and above by the small transverse or perpendicular sulcus y before referred to. The limitation anteriorly is continued downwards, in the same direction as y, to the horizontal sulcus which we have called w, along which the imaginary boundary runs backwards to the narrow gyrus surrounding the hinder end of this sulcus, and which bounds in front the vertical limb of the præcentral sulcus. Below w the border line of the area extends downwards parallel to the vertical limb of the præcentral sulcus, this portion of the line frequently corresponding with a small oblique sulcus which seems to us to be the anterior limb of the fissure of SYLVIUS. Posteriorly the area is limited by the vertical limb of the præcentral sulcus, and by a line continuing the direction of this same upwards to the middle line, passing a little in front of the anterior extremity of the sulcus x. The area of representation of this part has, therefore, roughly speaking, the outline of a flag, the staff of which forms the lower part (see fig. 3).

The synchronous conjugate deviation of the eyes to the opposite side is represented in the same region, but to a less extent than the movement of turning the head (*vide* page 212).

(II.) *The Lower Limb.*—The area of representation of the movements of the lower limb is limited in front by a line passing vertically through the anterior extremity of the sulcus x, and sometimes a little in front of this point; behind, it extends to the junction of the intra-parietal sulcus with the longitudinal fissure; upwards it extends to the median line, where it is continuous with the marginal convolution; below it is limited by the sulcus x, and by an imaginary line drawn backwards from this across the fissure of ROLANDO and through the middle of the sulcus z to the intraparietal sulcus. The shape of the area is in the form of a horizontal strip along the top of the hemisphere.

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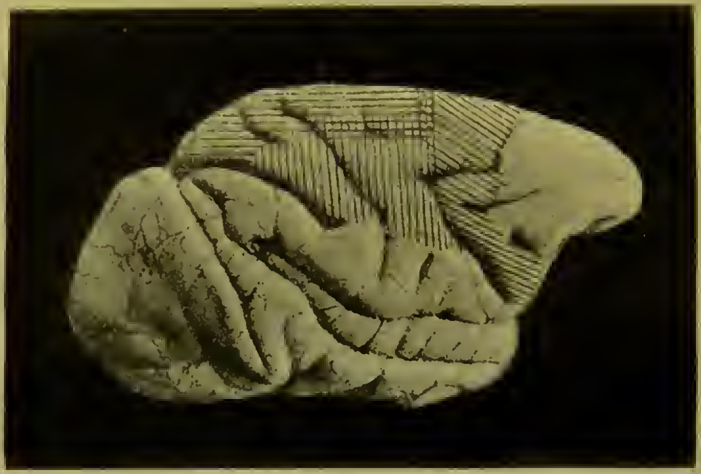
* By this is meant, of course, the turning away of the head so that the face looks away from the hemisphere stimulated.

Fig. 3.



A similar photograph, shaded to show the parts of the cortex, excitation of which produces movements of the head and eyes to the opposite side, and movements of the upper and lower limbs; it comprises the areas which were investigated in our previous paper, as well as those which are the subject of the present one.

Oblique shading represents the area of the movements of the head and eyes.
Vertical shading ,, ,, ,, upper limb.
Horizontal shading ,, ,, ,, lower limb.

The places where the lines, having different directions, intersect, denote the overlapping of the contiguous areas; and at these points the functions of these different areas are represented together.

(III.) *The Upper Limb.*—The area of representation of this limb we have already described in part in our former paper, in which, however, we left for future observation the analysis of the margins of the upper limb region. This we have now done, and we find that the upper limb is represented over the whole of the ascending parietal convolution below the line given above in limitation of the representation of the lower limb. For the discussion of the limitation of the rest of the upper limb region see page 238, where the localities of the fusion of the different contiguous centres are treated of in detail.

We do not here treat of the area of representation of the face, jaws, &c., and the observations on these points will form the subject of a future paper.

PART IV.—REPRESENTATION OF THE MOVEMENTS OF THE HEAD ACCOMPANIED BY CONJUGATE DEVIATION OF THE EYES. (Plate 40, figs. 3, 4, 4A, 5.)

The movements of the head and eyes were observed by Professor FERRIER as being simultaneous. We find on further analysis that, though this synchronous action is by far of commonest occurrence, yet that considerable differentiation exists, and of this we shall now speak, reserving the discussion of the simultaneous movements to pp. 213 to 215, when we consider the march of movements in this region.

The different movements, therefore, which have to be considered in this part are—

I. *Movements of the Head.*—The head moves in one of the following modes or in combination of the same:

(*a*) Simple horizontal rotation to the opposite side.
(*b*) Rotation with elevation of the muzzle.
(*c*) Rotation with adduction of head to the (opposite) shoulder.

II. *Movements of the Eyes.*—

(*a*) Both eyes open.
(*b*) Both eyes turn horizontally to opposite side.
(*c*) Both eyes turn to opposite side and upwards.
(*d*) Both eyes turn to opposite side and downwards.
(*e*) Both eyes return to the middle line (from the side stimulated) or turn only through a few degrees.

III. *Movements of the Pupils.*—

(*a*) Contraction.
(*b*) Dilatation.

I. *Movements of the Head:*

(*a*) Simple horizontal rotation to the opposite side. This occurs as a primary movement most markedly in the part of the cortex above the horizontal fissure of the præcentral sulcus, *i.e.*, the middle frontal convolution, and especially in the centres 32, and to a slightly less degree in 33, 40, 44, and 45 (see fig. 2). This movement of turning the head to the opposite side is also represented* over the whole area included by the centres 14–52.† From this it follows that the principal focus of the representation of this act, as a primary movement, is most marked at centre 32, from which point the representation gradually diminishes (*vide* fig. 4).

(*b*) Rotation to opposite side with elevation of the muzzle. It is a matter of common observation that the movement of the head to either side is often accompanied by a tilting of the head backward so that the face looks upwards as well as outwards. We have never observed this elevation of the muzzle below the horizontal limb of the præcentral sulcus. Further, this combined action, we find, is most represented in the superior frontal convolution close to the margin of the hemisphere, and most especially in the centre 48 ; in addition it is present in the centres 38, 47, 44, 45, 40, 41, 42, 34, and 35.

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* *I.e.*, absolute or total representation.

† Excepting, of course, centres 27, 30 (see pp. 242 and 244).

(*c*) Rotation with adduction of head to the opposite shoulder. In a few instances we noted that the rotation of the head was scarcely so marked as a rolling over and adduction to the opposite shoulder. This action was observed at 46 and 48 only, thereby showing that it occurs very rarely as a primary movement. It will be seen later on that it was observed occasionally as a secondary movement along the lower border of the horizontal limb of the præcentral sulcus.

II. *Movements of the Eyes :*

(*a*) Both eyes open. Before entering into the detailed account of the representation of this movement, we must observe that no great stress can with justice be laid on the frequency of the observation of this action ; for the reason that unless the animal be very profoundly narcotised the eyes remain open, while on the other hand, if it be so deeply narcotised, the cortex is no longer excitable to the currents we employ. With this reservation, we will now discuss the frequency and position of its occurrence. Since we have obtained this movement of opening the eyes at almost every point in which turning of the head is represented, we are inclined to believe that this movement constantly occurs in association with that of the head ; but, owing to the error of observation above referred to, we do not wish to speak more positively on this point. From two special experiments made to answer this question, we find that the movement was most represented at centre 32 ; from this point it diminished upwards and downwards, and especially in the former direction. With one doubtful exceptional case, the movement of opening the eyes is not represented along the middle line of the hemisphere or along the vertical line of centres immediately behind the sulcus *y*.

We are fortified in our opinion stated above by the fact that Professor FERRIER, in his work 'On the Functions of the Brain,' 2nd edit., p. 242, states that he obtained by stimulating his centre 12, which mainly corresponds to the region now under discussion, the following associated movements :—" the eyes open widely, the pupils dilate, and head and eyes turn to the opposite side."

(*b*) Both eyes turn horizontally to the opposite side. The eyes rarely turn to the opposite side as a primary movement ; this action is best represented in the convolutions situated in front of the præcentral sulcus, and to a less degree behind the sulcus *y*. Just as the movement of opening the eyes is associated with that for rotation of the head, so in like manner the turning of the eyes is found in connection with the same movement of the head.

The further consideration of this movement is continued under the heading of "March," *vide* p. 213.

(*c*) Both eyes turn to the opposite side and upwards. This movement was very rarely observed, and only in centres 15, 16, 17, 19, 20, and very slightly at 33 and 31.

(*d*) Both eyes turn to opposite side and downwards. This movement was noticed but twice, and only at centre 22.

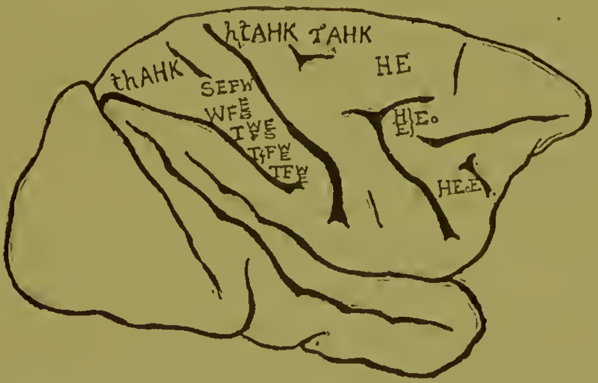
(*e*) Both eyes turn to the middle line, or only through a few degrees to the opposite side.

This action was observed to occur frequently in the centres 28, 28*a*, 26*a*, 26*b*. It consisted in a limited rotation of the eyes through a few degrees, such as would suffice to restore the direct position of the visual axes, if the eyes happened to be in position of slight conjugate deviation towards the hemisphere stimulated, and if any external strabismus happened to be present it was similarly instantly corrected.

In watching the rotation of the eyeballs we occasionally observed nystagmus of the eyes; this was only seen at the centres 15, 16, 29, and always consisted of rapid jerking movements towards the opposite side. This was probably merely a result of fatigue.

III. *Movements of the Pupils.*—In the vast majority of instances there was no movement of the pupils; when it occurred dilatation was always noted. This dilatation of the pupils exists simply in association with turning of the head and eyes to the opposite side. It appeared to be represented most round the horizontal limb of the præcentral sulcus, but we did not observe it many times.

Fig. 14.



This figure is illustrative of the march or sequence of muscular spasm at those points in the areas investigated which appeared to be most constantly the seat of origin of such sequence. The letters indicating the joints moved are placed in the order of the successive movements.

A = Ankle.
E = Eyes turning to opposite side.
E*o* = Eyes opening.
E = Elbow.
F = All fingers.
f = Index finger.
H = Head turning to opposite side.
H = Hip.
h = Hallux.
K = Knee.
S = Shoulder.
T = Thumb.
τ = All toes.
t = Small toes.
W = Wrist.

March or Sequence of Movement of the Head and Eyes. (See fig. 14.)

The relation of the movements of the turning of the head and eyes to the opposite side to that of opening the eyes varies as regards sequence of movement in the different parts of the cortex now under consideration. The sequence or order in which these movements occur forms the march for the part stimulated.

We shall take first the movements described above as an aid in dividing up the large area for the movements of the head and eyes, for the purpose of investigating the "March." It will be remembered that we postponed for later consideration the simultaneous movement of the head and eyes. The primary representation of this most important synergic action is given in Plate 40, fig. 5. It will be seen that its representation has a very wide distribution, which for the most part corresponds in mere extent with the representation of the movements of the head alone. As a primary movement, its importance entitles it to first consideration, for a review of the facts given in Table I.* will exhibit the very remarkable result that, of the 104 occasions on which this movement was observed to occur, in 100 instances it was primary. This is, no doubt, a demonstration of the necessity that this primitive movement should precede all others.

Taking first, then, the simultaneous movements of turning the head and eyes to the opposite side, the following march can be made out for a considerable number of centres. The order of this march is as follows :—

1. Simultaneous turning of the head and eyes to the opposite side.
2. Opening of the eyes wide.
3. Continuation of turning of the head.

And this occurs at centres 14 to 17 inclusive and 34.

The part next to be considered is the region below the sulcus *w*, which extends downwards in front of the vertical limb of the præcentral sulcus. The following movements here form the march :—

1. Turning of the head to the opposite side.
2. Opening of the eyes wide.
3. Turning of the eyes to the opposite side.

And are represented in the following centres, 19 to 28*b* inclusive. At the centres below *w* the opening of the eyes occurred earlier in the march than is just stated.

We would here direct special attention to the fact that occasionally the representation of the movements of the head and eyes is continued downwards, in front of the præcentral sulcus as far as its lower extremity, this area being limited in front by the subordinate sulcus (often very slightly marked) in the inferior frontal convolution, which probably represents the anterior limb of the Sylvian fissure.

We believe that it was owing to the very large proportion of negative results (*i.e.*, recorded nil) observed in stimulating this region, that Dr. FERRIER was led to consider it (*i.e.*, the part below the sulcus *w*) inexcitable.

We, however, find from a large number of observations that it is really excitable, although not invariably so. Of course, too, this excitability diminishes from above downwards. Not only is the representation in this region relatively less, but also the amount of movement evoked is much inferior in force and extent to that obtained in the centres above *w*.

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* See p. 242, *et seq.*

The relative amount of representation in the two parts is best shown by comparing the number of times in each in which no movement was obtained.

This will be made clearer by inspection of the following columns. In the left side are set forth, in position corresponding to their arrangement in the cortex, the centres above and below the sulcus *w*, viz., all those below the horizontal limb of the præcentral sulcus. On the opposite side of the central line are correspondingly arranged fractions, the numerators of which denote the number of negative results obtained, while the denominators give the number of observations on each particular centre.

	Centres.			Nils.		
	14	15	16	$\frac{0}{19}$	$\frac{1}{19}$	$\frac{1}{19}$
	17	18	19	$\frac{1}{16}$	$\frac{3}{16}$	$\frac{6}{17}$
Level of *w*						
	22	26	27	$\frac{2}{18}$	$\frac{13}{18}$	$\frac{17}{18}$[*]
	24	26′		$\frac{3}{15}$	$\frac{6}{14}$	
	28	26*a*		$\frac{3}{18}$	$\frac{5}{16}$	
	28*a*	26*b*		$\frac{4}{16}$	$\frac{7}{16}$	
	28*b*	26*c*		$\frac{7}{13}$	$\frac{5}{11}$	
	28*c*	26*d*		$\frac{6}{9}$	$\frac{3}{5}$	

(The thick black line in each group of figures denotes the level of the sulcus *w*.)

To return to the existence of marked inferiority of functional activity of this region, we would repeat that this is the part of the head and eye area where excitation evokes rotation of the head and eyes through only a few degrees, such, for instance, as is requisite to direct the face to the middle line, if it be a little diverted towards the side stimulated.

In discussing the bearing of the less forcible character of the representation in this region as compared with that around the horizontal limb of the præcentral sulcus, it must be observed that the negative results occurred in Monkeys with small brains, in which case consequently this portion of the brain was only slightly developed.

PART V.—REPRESENTATION OF THE MOVEMENTS OF THE LOWER LIMB. (See figs. 3, 6, 6A, 7, 8, 9, 10, 11, 12, 13, Plates 40 and 41.)

Before classifying and discussing the representation of the movements of the lower limb, it will be advisable to consider a few generalisations. In the first place, as we showed in our former paper, certain segments of the limb are of more importance than others; thus we demonstrated in the upper limb that its extremities, *i.e.*, the shoulder and the hand, possessed the greatest primary representation, the intermediate joints being only of subsidiary importance.

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[*] The one positive observation noted here was obtained in a Monkey in which the sulcus *w* was extremely short, so that centre 27 was brought near to the focus of representation.

It is interesting to find that the same phenomenon is present in the lower limb, the foot and the hip taking the lion's share of primary movement, while the knee, the intermediate joint, occupies quite a subordinate position. Indeed, in many cases it was obvious that the movement of the knee was only consequential to that of the hip, thus mechanically relieving the tension necessarily produced by flexion of the former joint.

The differentiation of the movements of the lower limb is not nearly so minute and distinct as in the upper limb. This is extremely well exemplified in the mode of sequence of the movements of the segments in the two limbs. For instance, in the upper limb excitation of the middle of the ascending frontal convolution* produces a comparatively slow and orderly successive flexion of digits, wrist, elbow, and shoulder; whereas excitation of the same convolution above and behind the posterior extremity of x evokes rapid movement of all the toes, almost instantly followed by movement of the ankle and hip with, as before remarked, the subsequent and subordinate movement of the knee. Indeed the rapidity with which movement of one segment followed that of another was so great as to make it appear that each, with the exception of the knee, was represented equally in point of time. In this way it was frequently difficult to discover the exact march of the spasm produced even by minimal stimuli.

Hence the march and also, as will be subsequently shown in detail, the primary movement, both show the same character of the representation of the lower limb as is revealed in the performance of so-called volitional efforts. Whereas the upper limb performs movements of great complexity and speciality of purpose, those of the lower limb are engaged in actions of a lower grade which are far less individualised.

We now proceed to discuss the seat of primary movement in each segment of the lower limb, as we have observed such to occur, and in each instance also the character of the movements evoked at each point excited.

The segments of the lower limb may best be considered in the order from below upwards, inasmuch as the smallest segments possess the most extensive primary representation.

For accuracy and convenience it is necessary to refer to the movements of the toes, not only under the two headings of hallux and the rest of the toes respectively, which, for further convenience, we shall speak of as the small toes, but also to the movements of all the digits acting simultaneously as a whole, under the expression "all toes."

The movements of the segments will consequently be described in the following order:—

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* Centre 3, *vide* former paper.

Hallux,
All toes,
Small toes,
Ankle,
Knee,
Hip.

In describing the movements of each of these segments we shall give (i.) the total or *absolute* representation in each instance, (ii.) the *primary* representation, (iii.) the character of the movements comprising (*a*) the total or absolute representation of the part, and (*b*) the primary representation.

By the expression *total or absolute representation* of any segment, we mean that we have extracted from our records every single movement of each given segment at every one of our centres where that segment happened to be represented. The summation of these facts gives correctly the actual total amount of representation of each joint at each centre, and consequently tells us to what extent, as determined by electrical stimulation, that joint or segment is represented in the cerebral cortex.

The second heading under which we have classified our observations, viz., that of *primary representation*, requires little explanation, since, unlike the first heading just described, it defines the region in which any particular joint begins the general movement of the limb, excluding, of course, secondary, tertiary, or even quaternary representations of the segment of the limb, all these being included under the first heading.

The determination of the representation of the primary movement is of the greatest importance, since upon this rests the exact localisation of the starting point of epileptiform convulsions.

Finally, by the *character of the movement* we mean whether it be one of flexion, extension, &c., and this is separately considered, according as the movement is referable to (*a*) absolute or (*b*) primary representation.

REPRESENTATION OF THE HALLUX (see Plate 40, figs. 6, 6A).

(i.) *Total or Absolute Representation.*—The movements of the hallux are represented[*] at the following centres in order of diminishing frequency :—

$$71,\quad \begin{Bmatrix}69\\68\end{Bmatrix},\quad \begin{Bmatrix}70\\62\end{Bmatrix},\quad \begin{Bmatrix}61\\65\end{Bmatrix},\quad \begin{Bmatrix}67\\64\\72\end{Bmatrix},\quad 59,\quad 55,\quad \begin{Bmatrix}54\\73\\75\\77\\6'\\6\end{Bmatrix}\quad 76,\quad \begin{Bmatrix}58\\52\end{Bmatrix}.$$

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[*] The centres enclosed vertically in brackets are those in which the degree of representation was equal.

On reference to Plate 40, figs. 3 and 6, it will be seen that this is tantamount to saying that the hallux is frequently represented all over the area for the movements of the lower limb, with the exception of its hindermost extremity, viz., centre 74. The maximum representation of the hallux is thus grouped round the upper end of the fissure of ROLANDO, and by reference to Table I., p. 250, &c., and fig. 6 it is evident that the representation of this segment decreases rapidly in intensity posteriorly, but more gradually anteriorly and inferiorly, reaching a minimum at each end of the lower limb area (*cf.* the region for absolute representation of "all toes"). The total number of times that the hallux was observed to move was 138.

(ii.) *Primary Representation* (see fig. 6A).—The hallux is primarily represented at

69, 68, 71, 62, 70, 61, 67, 65, 72, 75, 59, 58,

the centres being here arranged in order of decreasing intensity of representation.

It occurred to us that the order of these centres of primary representation ought to be decided by different considerations to those by which were determined the relative positions of the centres of *total* representation. Consequently we have gauged the intensity of the *primary* representation, not only by the greater proportionate* frequency with which it actually occurred, but also by its being accompanied or not by the occasional primary representation of other segments, *e.g.*, the small toes.

It will thus be seen that the hallux is represented in primary movement in a very large proportion of the centres which are relegated to the movements of the lower limb, in fact it occurs primarily in the proportion of over 50 per cent. While noting that the hallux is represented as a primary movement to such a degree, it is important to remember that its chief region of primary representation is close around the upper end of the fissure of ROLANDO. This latter generalisation not only assumes special importance in connection with the diagnosis of the seat of disturbance in an epileptiform convulsion beginning in the hallux, but also because it points to the fact, upon which stress will later be laid, that this part is the focal region of the representation of the lower limb. A total number of 82 primary movements of the hallux were observed.

III. *Character of Movement.*—(*a.*) *Absolute.* (*b.*) *Primary.*

We have found, somewhat unexpectedly, that there is no distinct localisation of any particular movement; extension and flexion † being apparently equally represented in any centre for movement of the hallux. It is true that there is a slight difference, according as the movement is a primary movement or not; thus we find that out of 82 instances of primary movement of the hallux, 47 were flexion adduction and opposition, *i.e.*, mainly flexion, while only 35 were the converse, viz., extension abduction.

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* By "proportionate" we mean the ratio of the primary movement of the hallux to all other primary movements occurring at the same segment (see p. 220, "Primary Representation of All Toes").

† In employing the term flexion of the hallux we have found it advisable to include therein not only direct flexion but also the more specialised movements of adduction and opposition. Although in this species of Monkey the hallux is employed as a thumb, nevertheless the special movements just mentioned were so frequently accompanied by the action of flexion, that the representation was most accurately described as that of flexion into the sole.

When, however, we come to enumerate the total or absolute number of instances in which the hallux moved, we find that this relationship is reversed, and that extension distinctly predominates. For instance, if we take the focus of representation of the hallux, viz., centres 69,71, and summate the absolute representation of movements, we find that "extension" occurs fifteen times, whereas "flexion" was observed only 6 times. Flexion is primarily represented at

$$70,\ \left\{\begin{matrix}69\\71\end{matrix}\right\},\ \left\{\begin{matrix}68\\67\end{matrix}\right\},\ \left\{\begin{matrix}61\\62\\72\end{matrix}\right\},\ \left\{\begin{matrix}65\\75\\59\end{matrix}\right\},\ 58;$$

while on the other hand extension is represented at

$$\left\{\begin{matrix}69\\62\\71\end{matrix}\right\},\ 61,\ 65,\ \left\{\begin{matrix}67\\72\\75\\77\end{matrix}\right\},\ \left\{\begin{matrix}70\\58\end{matrix}\right\}.$$

Hence, although flexion is the more frequent *primary* movement of the hallux, extension is the more important from an *absolute* point of view.

In our previous paper we drew attention to the combination of these movements as affecting the fingers, but in the lower limb it is most interesting to note that we have only observed extension of the hallux followed by flexion in one instance, viz., in Monkey 38, centre 64, where slight extension of the hallux preceded flexion. In connection with this it is proper to state that in Monkey 40 we thrice observed, viz., at centres 59, 61, 62, that adduction of the hallux was preceded by a slight movement of extension. The converse combination of these two exists, which merits attention, viz., the antecedence of extension by flexion—the movement of flexion being slight, and being instantly followed by a more powerful and permanent extension. When it is taken into account that the exceptional instances of flexion being preceded by extension are the only ones of the kind out of 138 recorded movements of the hallux, it is clear that some very remarkable relation exists between these two fundamental movements of this segment, though hitherto we have failed to discover any reason why the one combination should exist to the exclusion of the other—*cf.* representation of movement of toes, p. 222.

REPRESENTATION OF MOVEMENTS OF ALL TOES, ACTING SIMULTANEOUSLY.

(See Plate 40, fig. 7.)

(i.) *Total or Absolute Representation.*—The movement of all toes occurs at the following centres, in order of diminishing intensity,

$$71,\ 68,\ \left\{\begin{matrix}67\\58\end{matrix}\right\},\ \left\{\begin{matrix}69\\65\\61\end{matrix}\right\},\ \left\{\begin{matrix}73\\76\\77\\64\\54\end{matrix}\right\},\ \left\{\begin{matrix}62\\59\\52\end{matrix}\right\},\ \left\{\begin{matrix}72\\70\end{matrix}\right\},\ \left\{\begin{matrix}75\\6\end{matrix}\right\},\ 74,\ 6',\ 55.$$

Although we here give a list of the localities at which we have observed combined simultaneous movement of all the toes, we wish most particularly to remark that, on *a priori* grounds, it is not to be expected that such simultaneous movements should be as constantly localised as those of a highly specialised segment, like the hallux; further, we wish to draw attention to the fact that it may well happen that occasionally in those localities where the movement of the toes succeeds that of the hallux the time-interval may be so short that the movements are practically synchronous. For example, we have several times obtained, first, synchronous movements of all the digits; and, later, by carefully repeated minimal stimulation, discovered that occasionally there was a distinct interval between the movement of the hallux and the rest of the digits. It might have seemed justifiable to ignore those instances where the time-interval was exceedingly short, but we have thought it more accurate to record all the movements exactly as they occurred.

(ii.) *Primary Representation* of "all toes" occurs in diminishing intensity at centres,

$$77,\ 74,\ \left\{\begin{matrix}58\\52\end{matrix}\right\},\ 73,\ 54,\ 64,\ \left\{\begin{matrix}61\\67\end{matrix}\right\},\ 59,\ \left\{\begin{matrix}65\\72\\71\\76\end{matrix}\right\},\ 68,\ 70,\ 69.$$

We have drawn up the above list, as in the case of the hallux, according to the degree of intensity of the primary representation of "all toes" at any given centre.

This intensity has been estimated by taking the proportion of the primary representation of "all toes" as compared with frequency of occurrence of movement of other segments of the lower limb; these proportionate numbers have furnished the indices for each centre.

This order reveals a very definite symmetrical arrangement, not only constant as regards the position of the representation of all toes, but also with reference to the primary representation of the hallux. This latter, it will be remembered (see page 218), was grouped in greatest intensity round the upper end of the fissure of ROLANDO, this being the middle third of the lower limb area. In striking contrast to this (*cf.* figs. 6 and 7), we find that the representation of "all toes" is grouped at each extremity of the lower limb area, from which points it gradually diminishes in intensity towards the focus of representation for the hallux. Now, the hindermost centres of the lower limb area being 77 and 74, whereas 52 and 58 are the most anterior; these four centres are seen to head the above list of the primary representation of "all toes," showing that in the combination of the hallux and small toes forming the group of all toes, it is the smaller digits which take the larger share of the primary representation. Primary movement of "all toes" was observed 78 times.

(iii.) *Character of Movements.*

(*a.*) *Absolute.*—The first point of interest to be noted in the character of movements of "all toes" is that to which we drew attention, in discussing those of the hallux (p. 219), viz., that extension is the more frequent movement. Thus, out of 138 simultaneous movements of "all toes," only 21 were flexion, all the rest being extension. But a still more remarkable fact is brought out in considering the localities where these two opposite movements are represented; we have just seen that the simultaneous movement of "all toes" is most represented in positions exactly complementary to that of the hallux, it is now interesting to observe that the most important movement of the digits, *i.e.*, extension, is characteristic of the chief foci of representation of "all toes," while the far rarer movement of flexion is only to be found in those centres where the primary representation of "all toes" is overshadowed by that of the hallux.

The centres where flexion was most observed (arranged in successive order of decreasing importance) were :—

$$\left\{\begin{matrix}69\\68\\64\end{matrix}\right\},\ \left\{\begin{matrix}6\\76\\58\\67\end{matrix}\right\},\ \left\{\begin{matrix}70\\71\\65\\61\end{matrix}\right\}.$$

Comparison of figs. 6A and 8 with fig. 10 will show still more clearly than this list the relative position of the proportionate frequency of flexion.

(*b.*) *Primary.*—The character of the primary movement of "all toes" corresponds so closely with that of the absolute movement that it need not be separately considered.

Representation of Movements of Small Toes. (See fig. 10.)

(i.) *Total or Absolute Representation.*—Movements of the small toes we have observed to occur on excitation of the following centres, in order of decreasing intensity :—

$$62,\ 65,\ \left\{\begin{matrix}69\\67\end{matrix}\right\},\ 64,\ \left\{\begin{matrix}55\\59\\68\\70\\72\\73\end{matrix}\right\},\ \left\{\begin{matrix}78\\6'\end{matrix}\right\},\ 61,\ \left\{\begin{matrix}54\\74\\75\\76\\77\\6\end{matrix}\right\}.$$

On referring to Table I. for further details of this list, it is apparent how much less frequently the movement of small toes is represented than that of "all toes" or hallux, the figures being respectively 92, 138, and 138.

(ii.) *Primary Representation.*—The intensity of primary representation is given in the following order :—

$$78,\quad 55,\quad 64,\quad \left\{\begin{matrix}62\\72\end{matrix}\right\},\quad 67,\quad 65,\quad 73,\quad 74,\quad 6',\quad 77,\quad 6,\quad 70,\quad 76,\quad 69.$$

Owing to the comparative rarity with which primary movement of "small toes" occurs, it is necessary to be cautious in forming generalisations from this list; but it is abundantly clear that the fundamentally important generalisation which was so obviously true for the movements of all toes, also applies in the case of the small toes, viz., that the representation of the small toes is complementary to that of the hallux. For not only does movement of the small toes occur primarily but once at centre 69, and but twice at 70, where other primary movements occur to the number of 14 and 16 respectively, but also the "small toes," as such, are not so represented at 68 and 71. Primary movement of the small toes was noted 44 times.

At the same time it is evident, from the general rarity of primary movement of the small toes, that it is of very inferior importance among the movements of the lower limb. This conclusion is completely confirmed by observation of the so-called voluntary movements of the toes; primary simultaneous action of the small toes being extremely rare, and, perhaps, scarcely ever performed by Man, or by this species of Monkey.

(iii.) *Character of Movement.*

(*a.*) *Absolute.*—Again we find that, as in the case of "all toes," the movement of extension is much more largely represented than that of flexion. Thus, out of a total of 92 movements, 78 were extension and 14 flexion.

A further point of material interest in connection with this remarkable preponderance of the movement of extension is to be seen in the fact that the movement of flexion, when it happened, was observed only at centres

$$67,\quad \left\{\begin{matrix}68\\62\end{matrix}\right\},\quad 69,\quad 64,\quad 54,\quad 6';$$

these, with one exception, form a group immediately in front of the fissure of Rolando, and in the same region which we have already seen in the case of "all toes" to be connected especially with the flexion movements of those digits as well as the general representation of the hallux.

As we shall now leave the consideration of the movements of the toes for that of the movements of the ankle, it seems to us very desirable to make further reference to the fact just mentioned, viz., the peculiar localisation of the rare movement of flexion of the small toes in what we may call the hallux region of the lower limb area.

To put the matter in a simpler light than is offered by the bare record of observations, let us state again that the whole region of representation of the lower limb is a narrow strip running along and forming the upper fifth of the convex outer surface of the excitable region in the hemisphere; further, that the middle of this strip, or more strictly speaking, the junction of its middle and posterior thirds, is essentially the seat of representation of the hallux, while each extremity is essentially the seat of representation of the small toes.

To continue: the commonest primary movement of the hallux differs from that of the small toes in being flexion for the former and extension for the latter. Consequently we may say that, other things being equal, the movement of flexion will be characteristic of the more central portion of the lower limb area, while extension will be more marked at each extremity of this part. Under these circumstances it seems to us justifiable to entertain the belief that possibly a movement which is characteristic of any given segment in its focus of representation may be overshadowed by a different movement, if the representation of that segment is carried (diminishing in intensity, of course) into the focal region of some other segment whose characteristic movement is of an opposite nature. To be more particular, we would suggest then that this is the reason why flexion of the small toes is observed more frequently as the representation of those digits (whose characteristic primary movement is extension) invades, as it were, the region of the hallux (whose characteristic primary movement is flexion). We do not wish to press this point unduly, for the reason that the actual number of times that flexion of the small toes occurred is not large; but, as will be seen on reference to figs. 6, 8, and 9, the existence of this remarkable relation between the representation of flexion and extension in the toes is undeniable.

Representation of the Movements of the Ankle (Plate 41, fig. 11).

(i.) *Total or Absolute Representation.*—Movement of the ankle occurs in order of decreasing frequency at the centres—

$$68, 61, \left\{\begin{matrix}65\\72\end{matrix}\right\}, \left\{\begin{matrix}62\\67\\70\\71\end{matrix}\right\}, \left\{\begin{matrix}59\\76\end{matrix}\right\}, \left\{\begin{matrix}69\\73\end{matrix}\right\}, \left\{\begin{matrix}58\\64\\6'\end{matrix}\right\}, \left\{\begin{matrix}55\\77\end{matrix}\right\}, 54, 75, \left\{\begin{matrix}52\\78\\6\end{matrix}\right\}, \left\{\begin{matrix}51\\74\end{matrix}\right\}, 80.$$

On comparing these numbers with fig. 1, it is clear that the ankle is not specially represented in any one portion of the lower limb area, its focus only being situated in the centre of the area, and its intensity decreasing towards the borders with that of the limb generally.

The total number of times that we observed movement of the ankle was 198, a number which, as might have been expected, owing to the relative position of the joint in the limb, is far in excess of that of any other part.

(ii.) *Primary Representation.*—In marked contrast to the segments already described, primary representation of the ankle is of rare occurence, being observed only 36 times out of 198 actual movements. Although occurring so rarely, it is nevertheless important to remark that it was observed at no less than two-thirds (16 out of 23) of the centres in the lower limb area, thus again showing the general and subordinate character of the representation of this joint as compared with the focal character of that of others.

The infrequency of occurrence of primary movement of this joint diminishes, of course, the value of any arrangement in order of intensity of the same, and therefore we shall do no more now than state the arrangement we have found—

$$62, 59, 68, 74, \begin{Bmatrix}58\\61\end{Bmatrix}, \begin{Bmatrix}70\\72\end{Bmatrix}, \begin{Bmatrix}64\\69\\73\end{Bmatrix}, 77, \begin{Bmatrix}71\\76\end{Bmatrix}, 75, 6.$$

(iii.) *Character of Movement,*—(*a.*) *Absolute,*—The movements of the ankle are :—

(a.) *Dorsal flexion.* (By this we mean what is frequently called *flexion* of the joint, *i.e.*, when the toes are brought upwards, so as to approach to the front of the leg.)

(b.) *Plantar extension.* (By this we mean the opposite to dorsal flexion, *i.e.*, when the toes are pointed downwards, the heel being drawn upwards. This movement is frequently called *extension* of the ankle.)

NOTE.—We have preferred to employ these arbitrary terms as conveying a distinct notion of the direction in which the foot moves, thus, at the same time avoiding the homologically false use of the simple terms flexion and extension.

(c.) *Eversion.*

(d.) *Inversion.*

These movements (of an absolute total of 198) occurred in the following order of frequency :—

Dorsal flexion	116 times
Eversion	31 ,,
Plantar extension	26 ,,
Inversion	21 ,,

Confusion between dorsal flexion and plantar extension was noted in four instances.

The analysis of the localisation of the movements of dorsal flexion and plantar extension respectively gives no further information than that dorsal flexion is represented in proportion to the amount of general representation of the limb as a whole. Further that, apparently for the same reason, plantar extension was only observed in the middle of the lower limb area, especially since that part, as we have just shown, is essentially the region of representation of true, *i.e.*, homologous, flexion rather than of extension.

The movements of eversion and inversion deserve a passing notice. Their distribution in the lower limb area appears to be guided only by the relative degree of representation of the limb in the various parts of its cortical area.

In examining the question as to whether there exists any correlation between dorsal flexion and plantar extension, on the one hand, and eversion and inversion, on the other, we have found that the synergic relation between these movements was no more than the simple relation of probable frequency in proportion to the amount of actual representation of each. Hence it is impossible to make any generalisations on this point.

(*b*.) *Primary Movement.*—The number of times that primary movement was observed was 36. Of this number,

Dorsal flexion occurred	. .	14 times
Eversion ,,	. .	12 ,,
Plantar extension ,,	. .	8 ,,
Inversion ,,	. .	2 ,,

Beyond the obviously altered relation in the degree of representation which these movements bear to one another when primarily represented and when arranged in the order of the number of total representation, *i.e.*, all movements observed, there is nothing further to be remarked upon this point, save to mention that this small degree of primary representation is found, as might be expected, just in the middle of the lower limb area, *i.e.*, around and especially in front of the upper part of the fissure of ROLANDO.

REPRESENTATION OF THE MOVEMENTS OF THE KNEE (Plate 41, fig. 12).

(i.) *Total or Absolute Representation.*—Movement of the knee occurs in order of decreasing frequency at the centres :—

$$\left\{\begin{matrix}65\\68\end{matrix}\right\}, \left\{\begin{matrix}67\\71\end{matrix}\right\}, 70, \left\{\begin{matrix}54\\69\\73\\6'\end{matrix}\right\}, \left\{\begin{matrix}55\\64\end{matrix}\right\}, \left\{\begin{matrix}61\\62\end{matrix}\right\}, \left\{\begin{matrix}72\\77\end{matrix}\right\}, \left\{\begin{matrix}75\\76\\59\\6\end{matrix}\right\}, 58, \left\{\begin{matrix}52\\74\\98\end{matrix}\right\}.$$

The knee is thus represented all over the entire lower limb area, the total number of movements observed being 141 (*cf.* Ankle).

Further on we shall draw attention to the fact that the movements of the knee are essentially dependent upon those of the hip.

(ii.) *Primary Representation.*—The knee we have observed to move primarily only ten times, *i.e.* $\frac{1}{27}$th of the total primary movements of all the segments of the lower limb. And, moreover, of these ten times, in four it was associated with other synergic primary movements, *i.e.*, of hip and other joints. Consequently its *rôle* as a joint of primary movement is most insignificant, and we shall return to this question in discussing the representation of "purposive" actions of the limb.

(iii.) *Character of Movement.*—(a.) *Absolute.*—Of the total number of movements observed,

Flexion occurred	118	times
Extension ,, ...	12	,,
Rotation in ,, ...	7	,,

and confusion was noted in four instances.

The movement of extension, it is important to observe, occurred at the following centres in order of frequency :—

$$6,\ \left\{\begin{matrix}55\\61\end{matrix}\right\},\ \left\{\begin{matrix}54\\68\\69\\75\end{matrix}\right\},$$

and hence, though rare, it is represented about the same region as is the equally rare movement of flexion of the small toes, *i.e.*, close to the fissure of Rolando. This, as we have pointed out before, is the focus of representation of the limb, and perhaps the rare movements of extension and rotation in, which occur at the centres :—

$$68,\ \left\{\begin{matrix}6'\\6\\69\\70\\73\end{matrix}\right\},$$

owe their representation to the fact that, this being the middle of the lower limb area, the cortex here is most highly organised, and thus possesses centres for every movement of all the joints.

(b.) *Primary.*—The 10 primary movements of the knee were all flexion, with one exception, viz., rotation in.

Representation of the Movements of the Hip (see Plate 41, fig. 13).

(i.) *Total or Absolute Representation.*—Movement of the hip occurs in order of decreasing frequency at the centres :—

$$67,\ \left\{\begin{matrix}65\\6\end{matrix}\right\},\ \left\{\begin{matrix}61\\68\\71\end{matrix}\right\},\ \left\{\begin{matrix}55\\70\end{matrix}\right\},\ \left\{\begin{matrix}54\\62\\64\\73\\6'\end{matrix}\right\},\ \left\{\begin{matrix}59\\69\\72\\75\\76\end{matrix}\right\},\ 77,\ 58,\ 52,\ \left\{\begin{matrix}74\\78\end{matrix}\right\}.$$

The hip is thus represented most in the middle or focus of the lower limb area, moving altogether 177 times.

(ii.) *Primary Representation.*—The hip is primarily represented in the following centres in order of diminishing intensity :—

$$54, 76, 75, \left\{\begin{matrix}6'\\6\end{matrix}\right\}, 55, \left\{\begin{matrix}64\\65\end{matrix}\right\}, 52, 59, 61.$$

We must first call attention to the important deduction which these figures reveal, namely, that the hip is *primarily* represented in but 11 out of the 23 centres of its total or absolute representation; further that the centres, where it was observed to move primarily, are exactly the counterpart of those where the hallux is especially primarily represented. In accordance with the same fact, it is to be noted that behind the fissure of ROLANDO the hip is only represented in two centres, viz., 76 and 75, and that these centres are situated at the lower border of the area of representation of the limb. This localisation of the hip to the lower border of the area is equally strongly marked in front of the fissure of ROLANDO, and culminates in the fact that the centre in which most primary representation of the hip was found to occur is the lowest and most anterior of the whole lower limb group, viz., centre 54.* Primary movement of the hip was observed only 27 times.

(iii.) *Character of Movement.*—(a.) *Absolute.*—Of 177 movements,

Flexion occurred	118	times
Rotation out ,,	35	,,
Extension ,,	23	,,
Confusion ,,	4	,,
Abduction ,,	2	,,
Rotation in ,,	1	,,

Extension, remarkably rare in occurrence, was observed at the following centres in order of decreasing frequency—

$$6,\ 6',\ \left\{\begin{matrix}55\\61\\75\end{matrix}\right\},\ \left\{\begin{matrix}52\\64\\62\\69\\72\end{matrix}\right\}.$$

It is evident from these figures that this infrequent movement is most represented in the neighbourhood of centre 6, both behind and in front of the fissure of ROLANDO.

Rotation out occurs at centres :—

---

* Here we should remark that centre 51, although a border centre, where various parts of the body are represented (see p. 238), is also a centre where the hip is notably represented in primary movement (see also Table I.).

$$68,\ 59,\ \left\{\begin{matrix}65\\67\end{matrix}\right\},\ \left\{\begin{matrix}55\\61\end{matrix}\right\},\ 70,\ \left\{\begin{matrix}52\\58\\64\\72\\76\\6'\end{matrix}\right\}.$$

But there does not seem to be any definite localisation of the movements.

(b.) *Primary.*—Of the 27 primary movements :—

12 were flexion,
10 ,, extension,
5 ,, rotation out.

Flexion as a primary movement was most marked at 54 (6 times), then at 76 (twice), 59, 64, 6′, 75.

Extension was most marked at 6, then 75, 52, 61, 64, 61′.

Although so seldom moving primarily, it is interesting to note that when this did occur, the hip was nearly as often extended as flexed ; while on the other hand, as noted above, in the movements of the joint of secondary, tertiary, and quaternary sequence, extension was extremely rare as compared to flexion.

March or Sequence of Movements in the Segments of the Lower Limb.

(See fig. 14, p. 213.)

The sequence of movements successively invading the various segments of the limb, when any given point in the cortex is excited, varies in mode according to the segment in which the movement commences. For this reason the facts are best grouped together according to the seat of the primary movement. Thus we have different types named after the various segments of the limb. We commence with the most frequent.

Class I.—*Hallux Type*, observed at centres 61, 62, 65, 67, 68, 69, 70, 71, 72.

The march of the muscular spasm when commencing with movement of the hallux is very constant, the order of joints affected being almost invariably :—

Hallux, *Small Toes*, *Ankle*, *Hip*, and *Knee*.

In a relatively considerable number of instances the hip and knee moved simultaneously, and in one the movement of the knee preceded that of the hip.

The character of movement in the march was as follows :—

$\textit{Hallux}\left\{\begin{matrix}\text{flexed*}\\\text{or}\\\text{extended}\end{matrix}\right\}$; *Small Toes* extended ; *Ankle* dorsally flexed ; *Hip* flexed ; *Knee* flexed.

---

* Flexion more frequently than extension (see p. 219).

The general effect produced was thus, of course, a drawing up of the limb with extension of the digits. The movement of flexion of the knee might thereby gain a fictitious importance, if we did not at this moment explain that it was very frequently simply secondary to, and necessitated by, the flexion of the hip. It has already been pointed out what a very subordinate position the knee occupies among the joints of the limb, and especially that it is practically never primarily represented.

Class II.—"*All Toes*" *Type*, observed at centres 64, 58, 59, 72, 52, 54, 73, 77.

The character of the movement and the order was :—

All Toes extend ; *Ankle* dorsally flexed ; *Hip* flexed ; *Knee* flexed.

At each of the three last centres mentioned above there was once presented a slight variation in the order of the march ; but, being so infrequent, these variations were not deemed sufficiently important to merit separate description.

Class III.—"*Small Toes*" *Type*, observed at 55, 64, 78.

This type, only occurring three times, presents considerable confusion of arrangement, which deprives it of much importance. The localisation of the commencement of the march was fairly constant, viz., movement of the small toes, followed by that of the hallux. Consequent on the movement of the hallux we should naturally have expected movement of the ankle, and then of the hip and knee. At centres 64 and 78 this was indeed the case, but at centre 55 movement of the ankle terminated the march.

It will be remembered that in a few, comparatively rare, instances the ankle, knee, and hip commenced movement in the limb. It appeared to us likely that some interesting facts might be obtained by analysing these exceptional cases. This we did, and the results are best arrived at in the following order :—

(*a.*) *Ankle Type.*—The study of the march, when the movement is begun by the ankle, gave the following order, which was fairly constant, viz. :—

Ankle, Toes, Hip, Knee.

(*b.*) *Knee Type.*—Similarly, summation of the instances when the primary movement began in the knee was productive of the following result, as the most usual order of the march, viz. :—

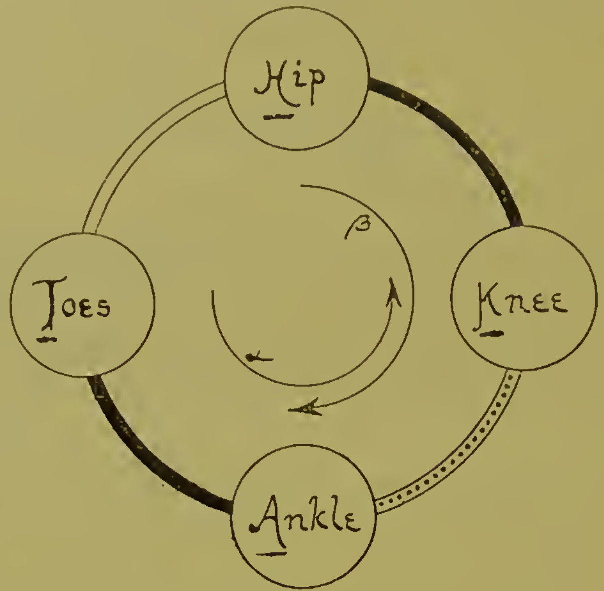
Knee, Hip, Ankle, Toes.

(*c.*) *The Hip Type.*—The commonest order of movement in this type was found to be :—

Hip, Knee, Ankle, Toes.

Comparison of arrangement in each of these more unusual marches with that of the common types described on pp. 228, 229 seems to us to suggest that the mechanism of a cortical motor centre is almost constant in arrangement, and that for the lower limb it may schematically be represented thus (fig. 15).

Fig. 15.



In this schematic figure the lines connecting the limb segments are made dark, dotted, or white to show the difference in amount or degree of association existing between the representation of the knee and hips, and between that of the ankle and toes respectively. (It must not be forgotten that this association is not only psychical in origin, but is also conditioned by the anatomical configuration of the muscles moving the various segments, whereby it happens, for example, that the hip cannot be notably flexed without similar movement of the knee, and again, that the powerful flexion of the toes causes plantar extension of the foot.)

Now the flow of energy which most frequently follows excitation is from T along the direction of the arrow α to H, but occasionally it is in the reverse direction, from H along the direction of the arrow β to T. This simple reversion of the current Dr. Hughlings Jackson fully described many years ago, as occurring in disease of the cortex in Man, and therefore we need not further consider it here. But, as we have just stated, in certain exceptional cases the flow of energy may start from A or from K. Of these two A is by far the more important, the movements of the knee being so very largely conditioned by those of the hip. Now, when the initial spasm affects the ankle, it is clear from the order in the ankle type of march that the energy flows in the more unusual direction of the arrow β, and so really simply continues the hip type of march. This mode of regarding the ankle type of march is of value as enabling us without exaggeration to harmonise what might otherwise appear to be conflicting observations.

Moreover, the *Knee Type* also probably conforms to the same system, although the order, viz., K, H, A, T seems at first sight to be wholly exceptional. The explanation of this may possibly be that the movements of the knee are so dependent on those of the hips as to bring their seats of representation in far closer connection than the union of the knee division of the area with its other neighbour (anatomically and schematically speaking) the ankle division. Hence, given the movement commencing in K, the course it will theoretically, and actually as observed by experiment, take is K, H, A, T, and not K, A, T, H.

PART VI.—REPRESENTATION OF THE MOVEMENTS OF THE UPPER LIMB.

In our former Paper in the 'Philosophical Transactions,' *loc. cit.*, we considered the representation of the upper limb as it occurred in the anterior half of the ascending parietal convolution. In the present paper we supplement our former account by a description of the movements obtained when the posterior half of that convolution is stimulated.

It will be useful if we now give in their positions the figures indicating the centres into which we divided the anterior half of the middle two-fourths of the ascending parietal convolution in our previous paper, and those of the posterior half adopted in the present research—

80	79	11
82	81	9
	83	8′
	85	8
	87	7′
		7

Above 80, 79, 11 is the parietal lobule. (See also fig. 2.)

In our former paper we contented ourselves with describing in one table the primary movement, the march, and the character of all the movements obtained. In the present instance, however, we shall follow the more minute arrangement adopted in the foregoing pages.

We shall now describe the movements of the various segments in the order of thumb, fingers, wrist, elbow, shoulder.

Representation of the Movements of the Thumb.

(See fig. 16, which with figs. 17, 18, 19, and 20 are extensions of the diagrams of the representation of the upper limb segments given in our former paper).

(i.) *Total or Absolute Representation.*—The thumb is represented along the posterior part of the ascending parietal convolution in the lowest four centres only, as follows, commencing with the most important, 87, 85, 83, 81.

The total number of times movement was observed was 40 (39 at centres 87, 85, 83).

(ii.) *Primary Movement.*—The thumb moved primarily at centres 87, 85, 83. It is most essential that we should here point out that at centre 87 not only did every movement of the thumb occur as a primary movement, but also that no other segment of the limb participated in such primary movement. It is further to be remarked that at centres 85 and 83 the primary movements almost equalled in number the absolute representation. (See Table I., p. 252.)

(iii.) *Character of the Movements.*—(a.) *Absolute.*—Of the 40 movements of the thumb,

26 were flexion and
14 ,, opposition.

Consequently the *general* movement of flexion of the digit into the palm was the only movement obtained.

(b.) *Primary.*—Of 37 movements,

25 were flexion and
12 ,, opposition.

These facts, coupled with those we noted in our previous paper, leave it beyond doubt that this region, viz., the middle third of the ascending parietal convolution, is the focus of representation of the movements of the thumb.

Representation of the Movements of the Fingers (See Plate 42, fig. 17).

(i.) *Total or Absolute Representation.*—The fingers are represented, in order of diminishing intensity, at the centres :—

$$85,\ 83,\ 87,\ 82,\ 11,\ \left\{\begin{matrix}79\\80\\81\\6\end{matrix}\right\},\ 6'.$$

It is worthy of remark that at 85 the representation of the fingers was found to be present 15 times, in contrast to 8 times at 87 and 7 times at 83.

The total number of movements observed was 54.

(ii.) *Primary Representation.*—Primary movement of the fingers was observed at the following centres, in order as before :—

82, 85, 83, 81.*

On close scrutiny we found that at centre 85 the index finger was primarily represented no less than 4 times in association with the thumb. The chiefest representation of the fingers all moving together is centralised at 82. Thus there exists, as might have been surmised, a gradation from above down of primary representation of all fingers, index, and thumb at the centres 82, 85, and 87 respectively.

---

* Note complete absence of primary representation of the fingers at centre 87.

(iii.) *Character of Movement.*—(a.) *Absolute.*—Of the total number of 54 movements,

35 were flexion,
15 ,, extension,
4 ,, "interosseal position."

At centre 85, where the greatest number of movements occurred, of 15 observations flexion occurred 14 times. And at 87 also flexion was alone obtained.

In striking contrast to this representation of flexion at the lowest part of this region, we find the movement of extension is alone represented at the highest part of the region, viz., at centres 11 and 79. In front of the fissure of Rolando, a somewhat different arrangement prevails at the upper part of the upper limb area. Here, as we showed in our previous paper, movement of the fingers occurred very slightly in degree and very late in time, and the character of this late and feeble movement was flexion. This fact we have now confirmed in our re-examination of the border centres 6 and 6′ (situated between the upper and lower limb centres).

(b.) *Primary.*—Of 11 movements,

4 were flexion,
3 ,, extension,
4 ,, abduction of the index.

The rarity of primary movement of the fingers here indicated is explicable by the fact that in the ascending parietal gyrus the movements of the fingers are almost universally secondary to those of the thumb. Thus of fifteen absolute movements of the "all fingers" (*i.e.*, excluding primary movements of the index), only 1 was a primary movement, and that was associated with the thumb. Reference also to the plate in our former paper and to fig. 14 shows this important preponderating influence of the thumb.

REPRESENTATION OF THE MOVEMENTS OF THE WRIST. (See fig. 18.)

(i.) *Total or Absolute Representation.*—The movements of the wrist are represented in the following centres, arranged in order as before :—

$$83,\ 85,\ \left\{\begin{matrix}87\\82\end{matrix}\right\},\ \left\{\begin{matrix}81\\80\\11\\6\end{matrix}\right\},\ \left\{\begin{matrix}79\\6'\end{matrix}\right\}.$$

The total number of movements observed was 40.

(ii.) *Primary Representation.*—The wrist initiated movement of the limb at the following centres :—

$$\left\{\begin{matrix}80\\81\\82\end{matrix}\right\},\ 83,\ 6',\ 85,\ \left\{\begin{matrix}11\\79\end{matrix}\right\},\ 6.$$

Altogether 16 movements were observed. The universality of representation of this joint in nearly all* the centres for the upper limb now under consideration, again demonstrates the condition described in our former paper, viz., that this joint is subordinate to the movements of the other segments of the limb, and notably to those of the digits.

(iii.) *Character of Movement.*—(a.) *Absolute.*—Of the 40 movements observed, no less than

21 were pronation,
14 ,, extension,
4 ,, supination,
1 was ulnar adduction.

Thus, while in no case was flexion observed, it is most noteworthy that pronation was the commonest movement. We would like again to quote the opinion expressed in our former paper as to the important part played by the movement of extension of the wrist in fixing the hand as a prefatory procedure in delicate movements of the digits, but we would insist that, even more than extension, pronation is absolutely essential to the correct performance of accurate and minute movements of the thumb and forefinger, the most highly specialised of the fingers. We therefore find the wrist represented immediately above (*i.e.*, preceding functionally) the areas for the latter segments. The movement of supination was noted at centres 87 and 85, but nowhere else, and occurred at the end of the act (*vide* March, *infra*).

(b.) *Primary.*—Of a total of 16 primary movements every one was pronation (*vide* March).

The intensity or degree of representation of this movement corresponds to the order given in (ii.) that of the primary representation of the joint.

REPRESENTATION OF THE MOVEMENTS OF THE ELBOW. (See Plate 42, fig. 19.)

(i.) *Total or Absolute Representation.*—The movements of the elbow are represented at the following centres, arranged in order of decreasing intensity :—

$$6,\ 11,\ 79,\ 6',\ 83,\ \left\{\begin{matrix}81\\82\\85\end{matrix}\right\},\ \left\{\begin{matrix}80\\87\end{matrix}\right\}.$$

The total number of movements observed was 50.

---

* Nine out of ten.

(ii.) *Primary Representation.*—The elbow initiated the movements of the limb in 9 instances at 7 centres :—

$$80,\ \left\{\begin{matrix}81\\82\end{matrix}\right\},\ 6,\ 6',\ 11,\ 83.$$

Proportionately we thus see that the elbow is very generally though feebly primarily represented (*cf.* the Wrist).

(iii.) *Character of Movement.* (a.) *Absolute.*—Of the 50 movements,

26 were extension,
23 ,, flexion,
1 was confusion.

These opposed movements were grouped thus : extension alone was obtained at 6 (12 times), 6′ (5 times), and 81 ; whereas flexion alone was obtained at

$$83,\ \left\{\begin{matrix}82\\85\end{matrix}\right\},\ 87.$$

At centres 11, 79, and 80, viz., the neutral ground between the two extremes just detailed, both flexion and extension were nearly equally represented, with, however slight predominance of the former.

(b.) *Primary.*—Of the 50 total or absolute movements of the elbow, only 9 were primary, this notably illustrating its subordinate importance. Of these, 6 were extension and 3 were flexion. The distribution of these primary movements was the same as that of the absolute movements.

Representation of the Movements of the Shoulder. (See Plate 42, fig. 20.)

(i.) *Total or Absolute Representation.*—Altogether 62 movements of the joint were observed, occurring at the following centres, in order of diminishing frequency :—

$$11,\ 79,\ 6',\ 81,\ 82,\ \left\{\begin{matrix}80\\83\end{matrix}\right\}.$$

The important fact here exhibited, namely, that the shoulder is not represented at centres 85 and 87, will not escape notice (*vide* March, *infra*). On the other hand, of 14 total primary movements at centre 79, the shoulder claims no less than 13 ; and for centre 11, out of a total of 14, it claims 12. Thus, the localisation of the shoulder, like that of the thumb, is very perfectly defined.

(ii.) *Primary Representation* —The shoulder, like the thumb, being an important joint in the initiation of movements, moved primarily 34 times at the following centres, in the order of diminishing intensity :—

$$79,\ 11,\ 81,\ 6,\ \left\{\begin{matrix}80\\82\end{matrix}\right\}.$$

(iii.) *Character of Movement.* (a.) *Absolute.*—Of the total of 62 movements,

28 were adduction,
15 ,, advancing,
11 ,, retraction,
4 ,, elevation,
3 ,, rotation in,
1 was rotation out.

Adduction.—Occurred at :—

$$11,\ 79,\ \left\{\begin{matrix}6\\81\end{matrix}\right\},\ \left\{\begin{matrix}80\\82\\83\end{matrix}\right\},\ 6'.$$

More than half (15) of the instances were observed at 11 and 79. The same thing was observed for the movement of retraction, the explanation probably being that these movements are associated, as we have shown in addition that this is the region of greatest representation of the joint.

Advancing.—This movement—one of great importance and interest—with the exception of being once observed at centre 82, was represented solely in front of the fissure of Rolando, namely, at 6 and 6′ (8 times and 6 times respectively).

Elevation was noted 3 times at 79 and once at 11 out of the total of the 4 occasions on which it was observed, thus being closely localised.

(b.) *Primary.*—Of the 36 primary movements of the shoulder (*i.e.*, including combinations),

22 were adduction,
9 ,, retraction,
4 ,, elevation,
2 ,, advancing.

Primary movement of adduction was observed at :—

$$\left\{\begin{matrix}11\\79\end{matrix}\right\},\ 6,\ 81,\ \left\{\begin{matrix}6'\\80\\82\end{matrix}\right\};$$

11 and 79 equally gave 7 instances of this movement, so that it was represented 14 times out of 22. Retraction occurs almost entirely at 11 and 79.

It will now be fitting to discuss the order of combination of the movements of the various segments.

MARCH OR SEQUENCE OF MOVEMENTS IN THE SEGMENTS OF THE UPPER LIMB (see Table II. and fig. 14).

As the centres in which the upper limb is represented are so few in number in the present research, we have deemed it best to give the march of the movements in full at each spot, in a tabular form.

TABLE II.

Centre.	Primary.	Secondary.	Tertiary.
11	Shoulder add., retract. .	Elbow flex.	Fingers extend. Wrist ext.
79	Shoulder, add., retract., elevate.	Elbow flex.	Fingers ext.
80	Border centre	See p. 238.	
81	Border centre		
82	Wrist pronated	Fingers interosseal flex.	Elbow flex. Shoulder adduct.
83	Thumb flexed, opposed .	Wrist pronated. Fingers flexed.	Elbow flexed. Shoulder add. (2)
85	Thumb flexed, opposed. Index opposed	Fingers flexed . . .	Wrist extend. Elbow flex.
87	Thumb flexed, opposed .	Fingers flexed . . .	Wrist extend, supinate. Elbow flex.

The march in this, the posterior half of the ascending parietal convolution, is more differentiated than that of the anterior half and, *a fortiori*, than that of the ascending frontal convolution.

In the upper part of the region it passes steadily down the limb, and in the lower part as steadily up the limb.

In this connection it is very important to observe the real position and value of the index finger. Thus, at centre 85 the march is very distinctly in the order of: thumb, index finger, the other fingers, wrist, and elbow. So at this part, where, as we have already seen, the index possesses some primary representation, it forms a distinct item in the march. Further, it is most noteworthy that the wrist is invariably pronated in the upper part of the region now under consideration. The importance of this fact has already been alluded to in considering the necessary succession of movements in the performance of the highly evolved actions of the thumb and index finger.

At the same time, it is of great interest, in connection with the development of psychical energy, to see that the representation of the shoulder does not proceed lower than centre 83, while at the same time also the representation of the thumb extends upwards to, but not beyond, the same centre.

Character of Movement in the March.

There are several differences in the character of the successive movements represented in the ascending parietal convolution and those in the ascending frontal convolution. Thus, the shoulder in the parietal gyrus, instead of exhibiting the representation of "advancing," as in the frontal gyrus, is almost invariably adducted and retracted (rarely elevated) at the centres 11 and 79.

PART VII.—MISCELLANEOUS FACTS.

There are several facts of general interest which have come to light in the course of our experiments.

(1) *The Border Centres* (see fig. 3).

We have employed this term to denote those centres which are situated along the lines separating continuous areas of representation.

The centres which come into this category are :—

31, 36, 37, 38, 39, 50, 51, 6, 6′, 80.

The representation of function at each of these centres is best seen by summing the absolute representation at each point, and the results of this method we shall now state.

Thus, for example, at centre 31—

Head turned to the opposite side	7	times
Head and eyes turned	3	,,
Eyes opened	5	,,
Eyes turned to opposite side	3	,,
Shoulder advanced	7	,,
Shoulder rotated	3	,,
Elbow extended	5	,,
Elbow flexed	2	,,
Wrist extended	4	,,

Thus centre 31 is clearly the seat of a simple fusion of the movements of the upper limb and those of the head and eyes. Centre 31 thus serving as an example, it will be similarly found on referring to Table I. that at—

Centre 36	We have fusion of the movements of the	Head and eyes and Upper limb.
,, 37 ,, 38 ,, 39	,, ,, ,, ,,	Head and eyes, Upper limb, Lower limb.
,, 50	,, ,, ,, ,,	Head and eyes, Upper limb, Lower limb.
,, 51	,, ,, ,, ,,	Head and eyes, Upper limb, Lower limb.
,, 6 ,, 6′ ,, 80	,, ,, ,, ,,	Upper limb, Lower limb.

From the extreme limitation of the effects of excitation in the thumb region, it is clear that the fusion of representation observed at the above described border centres cannot be due to spread of the current, but is to be interpreted as evidence of the gradual character of the evolution of representation of movements in the cortex. Such evolution would suggest the overlapping of the function of one region by that of another, and the more so in proportion as the parts are commonly moved in association.

(2) *Epilepsy.*

This we observed to follow the weak excitation, we always employed, at centres—

33, 40, 50, 51(2), 54(2), 58, 62, 65(2), 67, 68, 69, 6′, 72, 75.

(2) Noted twice.

It will thus be seen that the focus of the area of representation of the lower limb is the commonest seat of epileptiform disturbance. This may be due to the fact that the different regions of the lower limb area do not equally respond to the same stimulus, so that the same current just sufficient to evoke movement from one centre may cause overaction of another. Though it is undoubtedly a fact that some centres are more easily excited than others, still we do not put this prominently forward in any other sense than as a suggestion towards the interpretation of the above-described localisation of the tendency to the development of epileptiform convulsions.

(3) *Movements of Second and Third Toes.*

In Monkey 40, centre 65, and in Monkey 38, centre 68, the second and third toes began the movement of the limb, independently of the other toes. The movement in the first case was that of extension of the second and third toes, in the other it was that of opposition. Of course, in the Monkey, the second toe is the homologue of the index finger, and consequently is occasionally associated in movement with the hallux, as a primary movement; thus, at centres 65 and 68 in Monkeys 25 and 40 respectively, separation of these two digits was observed in the former, followed by extension of all the toes, while in the latter opposition took place. The march of the movements at these centres makes it quite clear that in these instances the second and third toes occupy undoubtedly a truly primary position, since movement of these is followed by that of all the other toes.

(4) *Purposive Movements.*

(a.) *Head and Eyes.*—It is well worth while to shortly review the so-called voluntary or purposive movements in the light of the facts detailed in the foregoing pages. In the first place, rotation of the head and eyes to one side is a necessary accompaniment of all the highest movements. This will probably explain the fact that this rotation of the head and eyes is represented over the whole breadth of the hemisphere reaching from near to the fissure of SYLVIUS below to the middle line above. It is thus in close apposition, from below upwards, to the areas for the face, the upper, and the lower limbs, respectively. It is, moreover, the area which intervenes between the presumably higher psychical centres of the præfrontal region and the lower areas for the face and limbs; hence, it seems probable that impulses proceeding from these higher centres will traverse the area for the head and eyes on their way to the areas for the limbs.

(b.) *Upper Limb.*—We can, with advantage, add to what we said about the movements of the upper limb in our former paper. Some of these movements we have already discussed in considering the mode of the march (p. 237), but to these considerations we would like to add one or two more of a wider nature. It is time to consider whether we cannot elucidate the fundamental principles which underlie the development of the mechanism for the performance of so-called voluntary actions. In the first place, we cannot pass by the obvious fact upon which we think we are now entitled to speak with some degree of certainty, viz., the suggestive difference between the functional activity of the ascending frontal and ascending parietal portions of the upper limb area.

While at the upper part (especially anteriorly) of the ascending frontal portion we find represented, as an initial movement, advancing of the whole limb with extension of all the joints, behind the fissure of ROLANDO the converse exists, and accordingly we find there the function of adduction and retraction of the shoulder with flexion of the elbow.

Summing all these facts together, we would advance the suggestion that an exact parallelism exists between the topographical relations just described and the sequence of movements in such a very frequent purposive action as that of, first, directing the gaze upon an object; next, reaching forward of the upper limb with extension of the joints to seize it; and, thirdly, the withdrawing of the arm with adduction of the shoulder, and carrying of the hand to the mouth by flexion of the elbow.

We are loath to lay too much stress on these deductions, as they are necessarily speculative, and also because we feel that a great deal has yet to be done in explanation of the fact that there are several movements relatively frequently performed by the head and eyes or the limbs, and yet which we have not been able to elicit by electrical stimulation from the regions in which they are presumably represented.

For instance, we have never observed the movement of direct upward rotation of the eyeballs, nor even circumduction of the shoulder, nor, to any marked degree, extension of the hip.

It seems to us probable that the absence of these special movements is owing to the method of analysis. The excitation of the so-called motor cortex by a faradic current is most obviously a very different effect-producing agency to the normal passage of a nerve impulse from the sensory perceptive areas, as occurs in the early stages of an effort of volition. What we mean, in short, is, that we cannot, with the present means at our disposal, apply a minutely localised excitation to one small group of corpuscles, and so cause them to discharge, without at the same time arousing into equal, or perhaps under certain circumstances even greater, activity other contiguous and possibly allied combinations of movements.

(5) *Opening of the Eyes.*

In one Monkey (No. 25) we observed in stimulating centres 32 and 33, that the two eyes did not open synchronously, but that the eyelids of the eye on the opposite side to that of the cortex stimulated opened before the eyelids of the same side. The time between the two movements was very slight, but still it shows that, although this movement is usually strictly bilateral, yet in exceptional instances the eyelids of the opposite side tend to act before those of the same side.

Abbreviations.

Hd. = Head.
Hd. E. } = Simultaneous deviation of Head and Eyes.
L. = Left, *i.e.*, opposite side to that stimulated.
E. = Eyes.
Sh. = Shoulder.

TABLE

Centre.	Primary movement.			Secondary.		Tertiary.
14	Hd. E. } 13	Hd. to L., 3 E. to L., 3-5		Eyes open, 4 Hd. to Sh., 1		
15	Hd. E. } 9	Hd. to L., 5 E. to L., 3		Eyes open, 2 Hd. to Sh., 3		
16	Hd. E. } 7	Hd. to L., 6 Eyes to L., 2 Eyes open, 3		Hd. to L., 3 Eyes to L., 4 Eyes open, 1 Hd. to Sh., 2		
17	Hd. E. } to L., 11	Hd. to L., 3 Eyes to L., 3 Eyes open, 1		Hd. to L., 3 Eyes to L., 2 Eyes open, 2 Hd. to Sh., 1		Hd. to Sh , 3
18	Hd. E. } to L., 7	Eyes to L., 2 Eyes open, 2 Hd. to L., 1 Hd. to Sh., 1		Hd. to L , 2 E to L., 2 Eyes open, 1 Hd. to Sh., 2		
19	Hd. to L., 5	Hd. E. } to L., 3 Eyes open, 2 Eyes up, 1		Eyes to L., 4 Hd. to L., 2 Eyes open, 1		Eyes to L., 2
20	Hd. to L., 7	Hd. E. } to L., 3 Eyes open, 3	Eyes to L., 1	Eyes to L., 5 Hd. to L., 2 Hd. E. } to L., 2		Hd. to Sh., 1
21	Hd. to L., 5	Eyes open, 1 Eyes to L., 1		Eyes to L., 2 Hd. to L., 1 Eyes open, 1		Eyes to L., 2
22	Hd. to L , 8	Hd. E. } to L., 5	Eyes to L., 2 Eyes open, 1	Eyes to L., 6 Eyes open, 2		Hd. to L., 1 Eyes open, 1
24	Hd. to L., 5	Eyes open, 3	Hd E. } to L., 2 Eyes to L., 2	Hd. to L., 2 Eyes to L., 2 Eyes open, 1		Eyes fixed, 1
26	Hd. to L., 2 Eyes open, 2	Eyes to L., 1		Eyes open, 2		
27	Eyes open and turn, 1 (Very slight and slow)					
26′	Hd. to L., 5	Eyes open, 3		Eyes to L., 3		
26*a*	Hd. to L., 6	Eyes open, 4	Hd. E. } to L., 1	Eyes open, 3 Eyes to L., 2 Hd. to L., 1		Hd. to L. (25°), 1 Eyes open, 1 Eyes straighten, 1
26*b*	Hd. to L., 5	Eyes open, 4		Eyes to L., 2 Eyes opon, 2 Hd. turns, 2		Hd. to L., 1
26*c*	Hd. to L., 2 Eyes to L., 2	Eyes open, 2				
26*d*	Hd. to L., 1 Eyes to L., 1					
28	Hd. to L., 7	Eyes open, 5	Hd. E. } to L., 2 Eyes to L., 1	Hd. to L., 2	Eyes to L., 1 Eyes open, 1	

Quaternary.	Nil.	Total.	Remarks.	Centre.
	0	19		14
	1	19	Weaker than 14 in 7 out of 18; nystagmus to L., 1	15
	1	19	Nystagmus, 1; eyes up and out (secondary), 1; horizontal (secondary), 1	16
yes up and out, 1	1	18	Less than 14, three times	17
	3	18		18
	6	17	Two cases more than 18	19
	4	18	Less than 14, 15, or 16, once; less than 14, once; greater than 16, once; eyes fixed, not turn, twice	20
	10	17	In one case included in the "nil" column the left ear retracted	21
	2	18	Eyes down, twice; eyes and head moved to opposite side in jerks	22
	3	15	All movements were slow and slight, and one noticed in jerks	24
	13	18		26
	17	18	The one positive result was probably due to "*w*" extending less posteriorly than usual	27
	6	14		26′
	5	16		26*a*
	7	16		26*b*
	5	11		26*c*
	8	5		26*d*
	3	18		28

TABLE

Centre.	Primary movement.			Secondary.		Tertiary.	
28*a*	Hd. to L., 6	Eyes open, 4	Hd. E. } to L., 1 Eyes to L., 1	Hd. to L., 3	Eyes to L., 2 Eyes open, 1		
28*b*	Hd. to L., 2 E. to L., 2 E. open, 2			Hd. to L., 1			
28*c*	Hd. to L., 1 E. open, 1 E. to L., 1			Hd. to L., 1			
29	Hd. to L., 4	Hd. E. } to L., 3	E. open, 1 E. to L., 1	E. to L., 2	Hd. E. } to L., 1 E. open, 1		
30	Hd. to Sh., 1 (?) E. open, 1 (?) E. to L. 1 (?)						
31	Hd. to L., 7	Hd. E. } to L., 3 E. open, 3	E. to L., 1 Wrist ext., 2 Sh. adv., 1	Hd. to L., 3 Elbow ext., 3	E. open, 2 E. to L., 2 Sh. adv., 2 Elbow flex., 2	Sh. adv., 4	
32	Hd. to L., 12	E. open, 1 Hd. to L. E. open } 1	Hd. to L. E. to L. } 1	E. to L., 5 E. open, 6		E. to L., 3 E. up, 2 Finger ext. Wrist ext. } 1	
33	Hd. to L., 10	E. open, 2 Hd. E. } to L., 2	Hd. to L. E. open } 1	E. to L., 7	E. open, 6	E. to L., 2	
34	Hd. E. } to L., 6	E. to L., 3 Hd. to L., 4	Hd. to L. E. open } 2	E. open, 4 E. to L., 4	Hd. to L., 1	Hd. to L., 2 E. to L., 1	
35	Hd. to L., 4	Hd. to L. E. to L. } 2 E. to L., 2	Hd. to L. E. open } 1 E. open, 1	E. to L., 2	Hd. E. } to L., 1 Hd. to L., 1		
36	Hd. to L., 6	Sh. adv., 4 Hd. E. } to L., 3	Wrist ext., 1 Toes ext., 1 E. open, 1	Elbow ext., 3	Sh. adv., 2	Elbow ext., 3	Wrist ext., 2
37	Hd. to L., 5	Hd. E. } to L., 2 Hip, 2 Ankle, 2	Sh. adv., 1 E. open, 1	See "Remarks"			
38	Hd. to L., 6	Hip rot. out, 1 Hip flex., 1 Ankle evert, plant. ext., 1					
39	Hd. to L., 7	Hd. to L. Eyes open } 3	Hd. E. } to L., 2 E. open, 1 Ankle evert., 1	E. to L., 4	Hd to L., 1 E. open, 1		
40	Hd. to L., 7	Hd. to L. E. open } 4	Hd. E. } to L., 3 E. to L., 1	E. to L., 4	E. open, 2		
41	Hd. to L., 7	E. to L., 3	Hd. E. } to L., 2 Hd. to L. E. open } 2 E. open, 1	Hd. to L., 3 E. to L., 3	E. open, 1 Hd. to L. E. open } 1		

I (continued).

Quaternary.	Nil.	Total.	Remarks.	Centre.
	4	16		28*a*
	7	13		28*b*
	6	9		28*c*
	6	15	Slight nystagmus at break of current	29
	11	14	Motor representation here probably very imperfect	30
Sh. rot. out, 3 Wrist ext., 2 Elbow ext., 2	1	18	As a tertiary movement, there occurred once each:—Hd. to L.; wrist extended; wrist pronated; flexion of fingers. As a quaternary movement, there occurred once each:—Hd. to L.; elbow flexed	31
	1	16	In Monkey 25, L. eye opened before R. at each of these centres. In 33 epilepsy noticed. Pupil dilated once	32
	2	17		33
	1	16	Muzzle up twice	34
	4	14	Muzzle up once. In two cases 35 < 34	35
	1	17	Fusion of movements of head and eyes with extension movements of upper limb occurred ten times. Movements of leg occurred twice	36
	3	16	There was fusion of head and eye movements with those of limbs, thus—with those of arm, 4; with leg, 3; with arm and leg together, 5	37
	5	14	No definite secondary movement, but there occurred twice:—extension of all toes, knee, and hip; and once each:—eyes open; eyes to L.; shoulder flexed; elbow extended; toes extended. As tertiary movement, once:—shoulder advanced, elbow extended; knee extended, confused. Muzzle raised up, 1	38
	0	14	As secondary movement there occurred once each:—shoulder advanced; elbow extended; hip and knee flexed; ankle inverted; toes extended. In one case there was observed after the secondary movement:—extended hallux; flexed hip and knee; arm advanced; head and eyes to L. In the primary movement of the eyes opening, occurring once, the L. eye opened before the R	39
	2	17	Muzzle raised up in two cases; pupils dilated in two cases; arm advanced late and slight in one case; leg once very late; L. eye open before R., once; epilepsy, once	40
	1	16	Pupil dilated, 1; muzzle raised up, 1; arm and leg affected together, but late, 1	41

TABLE

Centre.	Primary movement.			Secondary.		Tertiary.	
42	Hd. to L., 3 Hd. E. } to L., 3 E. to L., 3			E. to L., 3	Hd. to L., 1		
43	Hd. to L., 6	Hd. E. } to L., 1. Hd. to L. E. open } 1		E. to L., 3			
44	Hd. to L., 7	Hd. to L. E. open } 4	Hd. E. } to L., 1	E. to L., 7			
45	Hd. to L., 5	Hd. to L. E. open } 4	Hd. E. } to L., 3	E. to L., 5	E. open, 1	E. to L., 1	
46	Hd. to L., 4	Hd. E. } to L., 1	Hd. to L. E. open } 1 E. to L., 1	E. to L., 4	Hd. to L., 1 E. open, 1	E. to L., 2	
47	Hd. to L., 8	Hd. E. } to L., 1	Hd. to L. E. open } 1	E. to L., 4	E. open, 1 Sh. add., 1	E. to L., 1	
48	Hd. to L., 8	E. to L., 1 Hd. E. } to L., 1	Hd. to L. E. open } 1 E. open, 1	E. to L., 5	Hd. to L., 2 E. open, 1	E. to L., 1	
49	Hd. to L., 5	E. to L., 1	Hd. to L E. open } 1	E. to L., 2	Hd. to L., 1		
50	Hd. to L., 3 Upper limb, 5 Lower limb, 3	Hd. to L. Sh. adv. } 1			See "Remarks."		
51	Hip, 3 Hallux Toes } 3	Hd. to L., 2	Ankle dorso-flex., 1	Shoulder advanced, 3	E. to L. Hip flex., 1	Leg flexed, 1 Knee confused, 1 Ankle dorso-flex., 1	
52	All toes ext., 6	Knee flex., 1 Hd. to L., 1 Hip extend., 1	Sh. adv., 1 Hd. to L. E. open } 1	Ankle dorso-flex., 3	Sh. adv., 2 Hallux extend., 2 Hip rot. out, 1 E. open, 1	Hip flexed, 3	Hd. to L., 1 E. to L , 1
54	All toes extend., 7	Hip flex., 5	Knee flex., 3	Ankle dorso-flex. ,, invert. } 4	Hip flex., 2 Knee flex., 1 Hallux ext., 3 Hallux flex., 1 Small toes flex., 1 L. abdomen, 1 Arm, 1	Arm advanced, 8 Knee flex., 3 ,, ext., 1 Ankle dorso-flex., 1	
55	Small toes extend., 6	Hallux extend., 2 Hallux opposed, 2	Hip rot. out, 2 Hip flex., 1	Knee flex., 4	Ankle dorso-flex., 2 ,, ext. invert., 1 Hip flex., 1 Hip rot. out, 1	Ankle dorso-flex., 2 ,, invert., 1 Knee ext., 2 ,, flex., 1 Hip flex., 1 ,, ext., 1	Hip flex., 1 ,, ext., 1 Toes ext., 1 Hallux flex., 1

I (continued).

Quaternary	Nil.	Total.	Remarks.	Centre.
	6	15	Muzzle raised up, 2; Hd. to shoulder, 1; pupils dilated, 1	42
	6	14	Movements of head were associated with those of the arm and leg together, three times; with the arm only in two cases	43
	4	16	Muzzle raised up, 2. In one case there was:—ext. hallux, eversion ankle, flex. hip and knee. In another, L. hip was flexed and adducted	44
	4	16	Muzzle raised up twice	45
	5	12	Muzzle turned down at end of movement of turning head, 1. Hd. drawn to shoulder, once	46
	2	12	The upper limb was affected twice, and the lower limb, once. Muzzle raised up, 1	47
	3	15	Muzzle raised up, 3; arm and leg combined were affected, 1; Hd. drawn down to shoulder, 1	48
	5	12		49
	2	14	Epilepsy occurred once. This number being the border-land of the centres for movements of the head, the upper and lower limbs, it was impossible to find any definite march of movements, owing to the different results obtained	50
	1	10	Epilepsy occurred twice. The primary movements of the hip were extension, flexion, and abduction	51
	2	13		52
	1	14	Epilepsy twice in lower limb, not in the upper	54
Arm. adv., 5	3	14		55

TABLE

Centre.	Primary movement.			Secondary.			Tertiary.	
58	All toes ext., 6	Hallux flex., 1 „ ext., 1	Ankle invert. Ankle dorso-flex. } 2 Sh. adv. slight., 1	Ankle dorso-flex., 2 Ankle ext., 1 All toes flex., 2 Hip Knee } flex., 2	Hip abd., 1		Hip, 3	Knee, 2 Ankle, 2 Toes, 1
59	All toes ext., 4 Hallux flex., 1 „ ext., 2 „ add., 1 } 4	Ankle evert., 1 Ankle dorso-flex., 1 Ankle invert., 1 } 3	Hip and knee flex., 1	Ankle, 6	Small toes, 4	Hallux add., 2	Toes (small), 2 Hip flex., rot. out, 6	Knee, 3 Sh., 1
61	Hallux ext., 4 Hallux add. and opp., 3 } 7	All toes ext., 5 „ „ flex., 1 } 6	Ankle evert., 2 Ankle dorso-flex., 1 } 3 Hip ext., 1	Ankle invert., 7 Ankle dorso-flex., 2 Ankle plant. flex., 2	Small toes ext., 2 All toes ext., 1 Hallux add., 1 Hip rot. out. flex., 1		Knee flex., 3 „ ext., 2	Hip flex., 3 „ rot. out, 2 „ ext., 1 Sh. adv., 2 Toes ext., 1
6	Hip extend., 4 Sh. add., 3 „ retract., 1 „ adv., 1 } 5	Ankle evert., 1 Hallux ext., 2 Small toes ext., 1	Elbow ext., 2 Wrist pron , 1	Elb. ext., 5	Sh. flex., 1 Knee ext., 2 All toes flex., 2 „ „ ext., 2 }	Hallux ext., 2	Ankle plant. ext., 4 Ankle dorso-flex., 2 } 6 Hip ext., 3 „ rot. out, 1 } 4	Knee ext., 1 Sh. rot. in, 1 „ adv., 2 } 3 Wrist ext., 1
6′	Small toes ext., 2	Hallux ext , 1 abd., 1 opp., 1 } 3 Elbow ext., 1 Wrist pronat., 1	Hip rot. out flex. } 1 Hip ext., 1 Sh. add., 1 „ adv., 1 } 2	Hallux ext., 1 All toes ext., 2 Ankle dorso-flex., 1	Knee flex., 1 „ conf., 1 } 2 Hip rot. in, 1	Sh. adv., 1 „ rot. in, 1 „ add., 1 } 3 Elb. ext., 2 „ conf., 1 } 3 Fingers flex., 1	Small toes flex., 1 Ankle dorso-flex., 2 Knee ext., 1 Hip ext., 2	Sh. adv., 2 Wrist pron., 1
62	Hallux ext., 5 „ flex., 3 } 8	Small toes ext., 3 Small toes flex., 2 } 5	Ankle evert., 3 Ankle plant. ext., 1 Ankle dorso-flex., 1 } 5	Small toes ext., 4 „ „ flex., 1 „ „ conf., 1	Ankle invert., 2 Ankle dorso-flex., 1 } Hip flex., 2 „ ext., 1 } Hallux ext., 1 „ add., 1 }		Hip, 3 Ankle, 3 Toes, 4 Knee, 3	
64	Small toes ext., 5	All toes ext. and sep., 4 All toes flex., 1 }	Hip ext., 1 „ flex., 1 } Ankle evert., 2 Arm adv., 1	Hallux ext., 3 „ conf., 1 „ flex., 2 } 6	Ankle dorso-flex., 2 Ankle evert , 1 } 3 Small toes ext., 1 „ „ flex., 1 } 2 Arm adv., 1 „ add., 1 } 2		Knee flex., 4 Hip flex., 2 „ rot. out, 1 } 3 Ankle invert., 1 „ evert., 1 } 2	Hallux ext., 1
65	All toes ext., 3 „ „ flex., 1 } 4 Small toes ext., 4 Hallux ext., 3 „ flex., 2 } 5	Hip rot. out, 2		Ankle dorso-flex., 3 Ankle plant. ext., 1 Ankle evert., 1 „ invert., 1 } 6	Small toes ext., 4 Small toes flex., 2 } 6 All toes ext., 2 Hallux ext., 2 „ flex., 1 } 3 Knee flex., 2		Ankle invert., 4 Ankle dorso-flex., 1 } 5 Hip flex., 2 „ rot. out., 2 } 4 All toes ext., 2	Sh. 2
67	All toes ext., 4 „ „ flex., 2 } 6	Hallux flex., 2 „ ext., 2 „ opp., 3 } 7	Small toes ext., 2 Small toes flex., 2 } 4	Ankle dorso-flex., 4 Ankle plant. ext., 1 Ankle evert., 2 „ invert., 1 } 8	All toes ext., 3 Small toes ext., 1 Small toes flex., 1 } 2 Hip conf., 1 „ rot. out, 1 } 2		Hip flex., 2 „ rot. out., 3 } 5 Knee flex., 3 Small toes flex., 1 Small toes ext., 1 } 2	Ankle dorso-flex., 2 Ankle plant. flex., 1 Ankle invert., 1 } 4

I (continued).

Quaternary.	Nil.	Total.	Remarks.	Centre.
Hip rot. out, 1 Knee flex., 1 Arm, 1	1	12	Epilepsy once	58
Sh. adv., 3 All toes ext., 2 Ankle invert., 2	1	12		59
Sh. adv., 3 Hip flex., 2 Hip abd., 1 Elbow ext. and conf., 2 Knee, 1	0	16		61
Elbow ext., 5 Sh. adv., 4 Wrist ext., 1 Fingers flex., 3 Toes ext., 3 Knee and hip flex., 3 Hip ext., 2 Pelvis rot. to L., 2 Knee conf., 1 ,, ext., 1	1	13		6
Small toes ext., 1 Knee and hip flex., 2 Pelvis rot., 1 Sh. adv., 2 Elbow ext., 2 Fingers flex., 1	1	12	Epilepsy occurs once	6′
Toes, 2 Knee, 3 Ankle, 1 Hip, 2 Arm, 4	0	13	Epilepsy occurred once. It is to be noted that, among the small toes, those which were most represented were the 2nd and 3rd, and the 2nd more than the 3rd. In two cases the hallux and 5th toe were associated as a primary movement, but the 4th toe never	62
Arm adv., 3 Hip and knee flex., 3 Toes flex., 2	1	14		64
Hip and knee flex., 6 Knee flex., 3 Ankle, 2 Arm, 2	0	16	Epilepsy occurred twice. Note 2nd and 3rd toes	65
Knee, 7 Hip, 6 } conf. and flex. Sh., 4	1	17	Epilepsy once	67

TABLE

Centre.	Primary movement.			Secondary.		Tertiary.	
68	Hallux flex., 5 ,, ext., 5 } 10	All toes ext., 3 ,, ,, flex., 1 } 4	Ankle plant. ext., 3 Ankle dorso-flex., 1 } 4	All toes ext., 4 ,, ,, flex., 1 ,, ,, conf., 1 } 6 Small toes ext., 3 Small toes conf., 1 Small toes flex., 1 } 5	Ankle dorso-flex., 2 Ankle evert., 1 Ankle plant. ext., 1 } 4 Hip rot. out, 2 Hallux flex., 1 ,, ext., 1 } 2 2nd toe opp., 1	Ankle dorso-flex., 3 Ankle plant. ext., 1 Ankle conf., 1 ,, invert., 2 ,, evert., 1 } 8	Small toes flex., 2 Knee ext., 1 ,, flex., 1 } All toes flex., 1 ,, ,, ext., 1 }
69	Hallux flex., 6 ,, ext, 3 Hallux and 2nd toe ext, 2 } 11	All toes ext., 1 Small toes ext., 1	Ankle evert., 1 Ankle plant. ext., 1 } 2	All toes ext, 2 ,, ,, flex., 2 } 4	Small toes ext, 3 Small toes flex., 1 } 4 Ankle dorso-flex., 2 Ankle plant. ext., 1 } 3 Hallux ext., 1	Small toes ext, 2 Small toes conf, 1 } 3 All toes ext., 1 ,, ,, flex., 1 } 2	Hip and knee ext., 1 Hip and knee flex., 1 } 2 Ankle plant. ext., 1 Ankle dorso-flex., 1 } 2
70	Hallux flex., 7 ,, abd., 1 } 8	Small toes ext., 2 Knee flex., 2 ,, rot. in, 1 } 3 Ankle evert., 1 Ankle dorso-flex., 1 Ankle plant. ext., 1 } 3	All toes ext., 1 ,, ,, flex., 1 } 2	Small toes ext., 4 All toes ext., 2 Hallux ext., 2 Ankle dorso-flex., 1 Ankle plant. ext., 1 Ankle evert., 1 } 3	Hip flex., 1	Ankle dorso-flex, 5 ,, confusion, 1 } 6 All toes ext., 1 Sh. rot. out, 1	
71	Hallux flex., 6 ,, ext., 5 } 11	All toes ext., 4 ,, ,, flex., 1 } 5	Ankle dorso-flex., 1 Ankle plant. flex., 1 } 2	All toes ext., 9 Hallux ext., 4 Ankle dorso-flex, 3 Ankle evert., 1 ,, invert., 1 } 5	Hip flex., 3 Knee flex., 2	Hip and knee flex., 5 Ankle dorso-flex., 4 ,, conf., 1 } 5	
72	All toes ext., 5 Small toes ext, 5 Hallux flex, 3 ,, ext., 2 } 5	Ankle plant. ext., 1 Ankle dorso-flex., 2 } 3		Ankle dorso-flex, 3 Ankle plant. ext., 1 } 4	Hallux ext., 2 Knee and hip flex., 1	Ankle dorso-flex., 5 ,, invert., 1 } 6 Knee and hip flexed, 4	
73	All toes ext., 7	Small toes ext, 3	Ankle dorso-flex., 2 Hallux ext., 1 ,, flex., 1 } 2	Ankle dorso-flex., 6	Hallux ext., 2 Small toes ext, 2 Hip and knee flexed, 3	Knee and hip flexed, 3 Ankle evert., 1 ,, dorso-flex., 1	
74	All toes ext., 3	Small toes ext., 1 Ankle dorso-flex., 1		Ankle Knee Hip } flex., 1			
75	Hallux flex., 2 ,, ext., 2 } 4	Hip ext., 2 Sh. add., 2	Knee and hip flex., 1 Ankle evert., 1	All toes ext., 3 ,, ,, flex., 1 } 4	Small toes ext., 1 Knee ext., 1 Ankle evert., 1 Ankle dorso-flex., 2 } 3 Knee and hip flex., 1	Knee and hip flex., 1 Arm add. adv., 1	
76	All toes ext., 2 Hallux ext., 1 ,, flex., 1 } 2 Hip flex., 2	Small toes ext., 1 Knee flex., 1 Ankle dorso-flex., 1		Ankle dorso-flex., 3 Ankle invert., 1 } 4	All toes ext., 1 ,, ,, flex., 1 } 2 Hallux ext., 1 Hip flex, 1	Ankle evert., 2 ,, conf, 1 Ankle plant. ext., 1 Ankle dorso-flex., 1 } 5	Hip rot. out, 1
77	All toes ext., 5	Small toes ext., 1 Hallux ext., 1 Ankle dorso-flex., 1		Hallux ext., 3	All toes ext., 2 Ankle dorso-flex, 2 Hip flex., 1	Ankle dorso flex., 2 ,, evert., 1 } 3 Knee and hip flex., 1	

I (continued).

Quaternary.	Nil.	Total.	Remarks.	Centre
Hip rot. out, 5 Hip and knee flex., 4 Ankle, 3 Knee flex., 3 „ conf., 2 } 5	0	16	Epilepsy occurred twice. The 2nd and 3rd toes, in Monkey 38, opposed towards hallux as a primary movement	68
Hip and knee flex., 5 Ankle dorso-flex., 3 Knee at 90°, 1 Toes confused, 1	0	15	Epilepsy once	69
Hip and knee flex., 5 Knee confused, 1 Hip abd., 1 „ rot. out, 2 } 3 Arm adv., 2	0	18		70
Knee and hip flex., 3 Arm abd., 2	1	18		71
Hip flex., 1 „ ext., 1 } 2 Toes sep., 1	1	18	Epilepsy once	72
Hip rot. out, 1 „ flex., 1 } 2 Knee flex., 1 „ rot. in, 1 } 2	4	18		73
	8	14		74
	5	17	Epilepsy once	75
Hip and knee flex., 3 Toes sep., 2 All toes flex., 1 Ankle evert., 1	9	17		76
Hip and knee flex., 3 Knee flex., 1 Sh adv., 1	9	17		77

TABLE

Centre.	Primary movement.			Secondary.			Tertiary.	
78	Small toes ext., 4			Ankle dorso-flex., 2 Hallux ext., 1			Ankle dorso-flex., 1	
11	Sh. add, 7 „ retract., 4 „ elevated, 1 } 12	Wrist pronated, 1 Elbow ext., 1		Elbow flex., 5	Sh. add., 1 „ retract., 1 „ rot. in, 1 } 3	Elbow ext., 1	Fingers ext., 4 Wrist ext., 2	Sh. rot. out, 1 Hip ext., 1
79	Sh. add., 7 „ retract., 3 „ elevation, 3 } 13	Wrist pronated, 1		Elbow flex., 5	Fingers ext., 3 Elbow ext., 2		Wrist ext., 1 Hip ext. rot. in, 1	
80	Wrist pronated, 2	Elbow ext., 1 „ flex., 1	Sh. add., 1 Small toes ext., 1	Fingers inteross. ext., 2	Ankle dorso-flex., 1 Sh. add., 1		Wrist ext., 1 Fingers ext., 1	
81	Wrist pronated, 2 Sh. add., 2	Elbow ext., 1 Fingers ext., 1		Sh. retract., 1 Elbow ext., 1	Thumb and fingers flex., 1		Sh. add., 1 Elb. ext. conf., 1 Wrist ext., 1 Fingers flex., 1	
82	Wrist pronated, 2	Sh. add. retract., 1 Elbow flex., 1 Fingers flex., 1 „ ext., 1 } 2		Wrist pronated, 2 Fingers inteross. ext., 2			Wrist ext., 1 Elbow flex., 1 Fingers ext., 1	
83	Thumb flex., 5 „ opp., 2 } 7	Wrist pronated, 4 Fingers flex., 2 „ ext., 1 }	Elbow flex., 1	Fingers flex., 3 „ ext., 1 Index opp., 1 } 5	Wrist ext., 2 Wrist ulnar add., 1 } 3 Sh. add., 1		Elbow flex., 3	Wrist ext., 1 Fingers ext., 1 Sh. add., 1
85	Thumb flex., 10 „ opp., 4 } 14	Index opp., 4	Wrist pronated, 2 Fingers flex., 1	Fingers flex., 8	Index flex., 2 Thumb opposed, 2 Index opposed, 2 Fingers and thumb, 1 Wrist supin., 1		Fingers flex., 2 „ ext., 1 } 3 Wrist ext., 1 „ pron., 1 „ supin., 1 } 3	
87	Thumb flex., 10 „ opp., 6 } 16			Fingers flex., 8	Wrist supin., 1		Wrist ext., 2 „ pronat., 1	Elbow flex., 1

I (continued).

Quaternary.	Nil.	Total.	Remarks.	Centre.
Knee and hip flex., 1	7	11		78
Elbow ext., 1	1	12		11
	4	14		79
	12	16		80
	6	11		81
Sh. adv., 1 } 2 ,, add., 1 } Elbow flex., 1 All fingers ext., 1	8	15		82
Elbow flex., 1	3	17	Index finger opposed towards thumb, once as a secondary movement	83
Elbow flex., 3 Fingers flex., 1 Wrist ext., 1	3	19	Index finger opposed four times as a primary movement. Index finger flexed twice and opposed twice as a secondary movement	85
Wrist supin., 1 Elbow flex., 1	2	16		87

Description of Plates 40–42.

PLATE 40.

The figs. 4 to 13 and 16 to 20 are stippled to show the representation of the absolute movements and the primary movements of the different joints. In all of these the intensity of the stippling denotes the degree of representation of the movements of the joint.

Fig. 4 shows the area of absolute representation of turning the head to the opposite side. The points of greatest intensity are seen to be just above the horizontal limb of the præcentral sulcus, and the part next to the longitudinal fissure. The area is seen to be very extensive.

Fig. 4A gives the representation of the primary movement of rotation of the head to the opposite side. When compared with fig. 4 it is seen that the point of greatest intensity here is also just above the horizontal limb of the præcentral sulcus, and also next to the longitudinal fissure. In the corner formed by the two limbs of the præcentral sulcus the representation is faint, as this is the place where the simultaneous movement of the head and eyes is most marked.

Fig. 5 shows the representation of the primary movement of the simultaneous action of turning the head and eyes to the opposite side. The point of greatest intensity is in the angle formed by the two limbs of the præcentral sulcus, and is in counter-distinction to fig. 4*a*, where this part has only a feeble representation of the primary movements for rotation of the head.

Fig. 6. Here the absolute representation of the movements of the hallux are given. The greatest intensity is seen to be in front of the upper end of the fissure of Rolando, and to a less degree behind this end of the fissure; from these points the representation extends over the whole of the lower limb area, but in a very feeble degree.

Fig. 6A. The representation of the primary movement of the hallux is here seen to be localised almost entirely to each side of the upper end of the Rolandic fissure, and to have its seat of greatest intensity immediately in front of the fissure. The localisation is very sharply defined, and is more exact than any other joint of the lower limb. (*Cf.* figs. 7, 8, 9, and 10.)

Fig. 7 gives the absolute representation of all the toes acting together; the representation extends over the whole area for the lower limb, and has its greatest intensity just in front of and behind the most intense representation of the hallux.

PLATE 41.

Fig. 8. The representation of the movement of flexion of all the toes is here given, and it is seen to be almost entirely in front of the fissure of Rolando.

Fig. 9 gives the absolute representation of the movements of the small toes; the greatest intensity is seen to be in front of the fissure of Rolando, but in front of and below the part occupied by the hallux.

Fig. 10 shows the primary representation of the movements of the small toes, and, when compared with fig. 6a, it is seen to occupy that part of the area of the lower limb, which is not occupied by the representation of the primary movement of the hallux, *i.e.*, immediately in front of and behind the upper end of the fissure of Rolando.

Fig. 11 shows the absolute representation of the movements of the ankle. It is well marked over the whole of the lower limb area, and is better represented than the next joint, the knee (*cf.* fig. 12). Its greatest intensity is above the hinder end of the sulcus x, and in front of the area for the hallux.

Fig. 12 is the absolute representation of the movements of the knee; it has no special characters, but is fairly evenly distributed over the whole of the lower limb area, in conformity with the secondary character of the movements of this joint.

Fig. 13. The absolute representation of the movements of the hip is here given. While it extends over the whole lower limb area, it is most marked in front of the fissure of Rolando, and especially in the more anterior part; its greatest intensity here is further forward than the representation of the ankle (*cf.* fig. 11), and it is only slightly represented just in front of the fissure of Rolando, the area for the hallux.

PLATE 42.

Fig. 16 gives the absolute representation of the movements of the thumb as observed in the present research. It is seen in a very striking manner to be limited to the lower end of the intra-parietal sulcus and over a small area; its lower edge is sharply defined and its upper border exhibits only a very slight amount of shading off into the contiguous centres. It is the most highly defined of all the segments of the limb.

Fig. 17 shows the absolute representation of the movements of the fingers; it extends more or less over the whole upper limb area (examined in this present paper), and it is more extensive than the representation of the movements of the thumb (*cf.* fig. 16). But while it is only slightly represented in the upper part of the upper limb area, it is very marked at its lower part, and it will be noted that its point of greatest intensity is just above that of the representation of the thumb.

Fig. 18. The absolute representation of the movements of the wrist is here seen to extend over the whole upper limb area (here examined), and to be feebly represented at the upper part of this area, but to have its greatest intensity about the middle and just above the point of greatest representation of the fingers (*cf.* fig. 17).

Fig. 19 gives the absolute representation of the movements of the elbow. Though it is represented over the whole upper limb area (examined in this paper), it is very slightly marked in the part opposite the lower end of the intra-parietal sulcus; its chief seat being at the upper end of the upper limb area, on a level with the sulcus x, and its point of greatest intensity is at this level, immediately in front of the fissure of ROLANDO, and, to a less degree, in the contiguous part behind this fissure.

Fig. 20. Here the absolute representation of the movements of the shoulder is seen to be localised almost entirely to the upper limit of the upper limb area. It is most important to observe that the shoulder, alone of all the joints of the upper limb, is not represented at all in the lower part of this area, opposite the lower end of the intra-parietal sulcus—the seat of representation of the movements of the thumb and the fingers (*cf.* figs. 16, 17). The point of greatest intensity is seen to be in front of and behind the fissure of ROLANDO at the horizontal level of the sulcus x, the upper limit of the upper limb area.

On comparing figs. 16–20, it will be seen that the most intense representation of the movements of the segments of the upper limbs is arranged in a most perfect gradation from below upwards. The representation of the thumb occupies the lowest part of the upper limb area, *i.e.*, opposite the lowest point of the intra-parietal sulcus; the fingers have their seat of greatest intensity immediately above that of the thumb; the representation of the wrist is situated just above that for the fingers; while the elbow is represented higher up than the wrist, near the upper limit of the area. The representation of the shoulder forms the upper limit of the upper limb area, being localised rather higher up than that for the elbow.

It will also be noted as most important that, whereas the representation of the thumb is confined entirely to the lowest part of the upper limb area, the shoulder is represented almost entirely at the uppermost limit of this area, *i.e.*, the two extreme segments of the upper limb are limited in their representations to the extreme ends of the area.

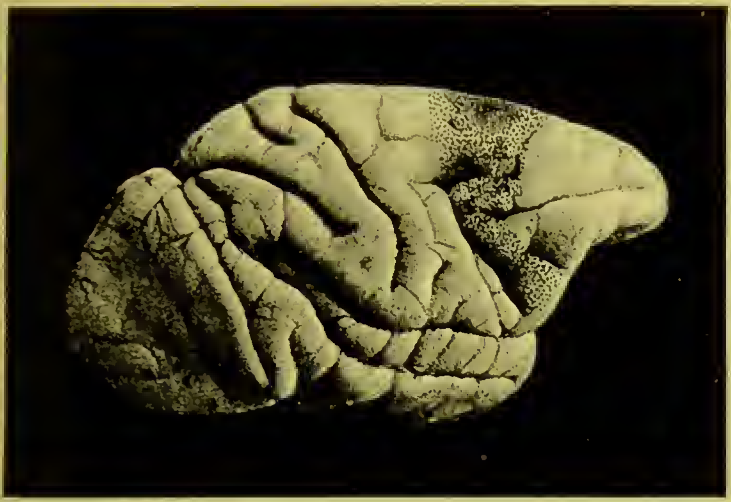


Fig. 4.—ABSOLUTE REPRESENTATION OF TURNING OF THE HEAD TOWARDS THE OPPOSITE SIDE.

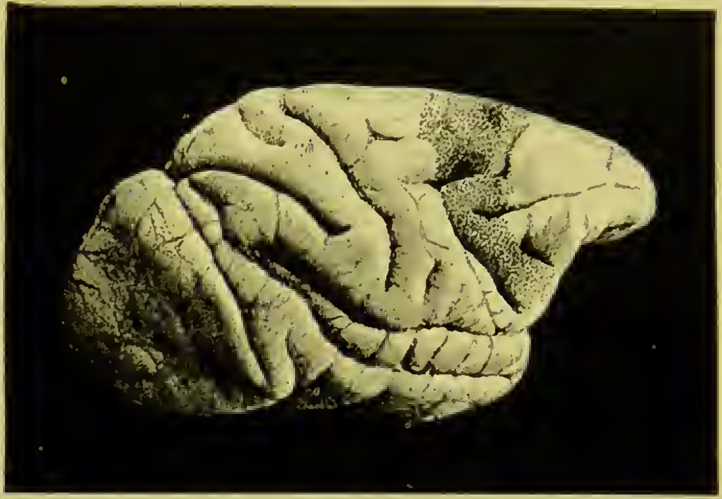


Fig. 4*a.*—PRIMARY REPRESENTATION OF TURNING OF THE HEAD TOWARDS THE OPPOSITE SIDE.

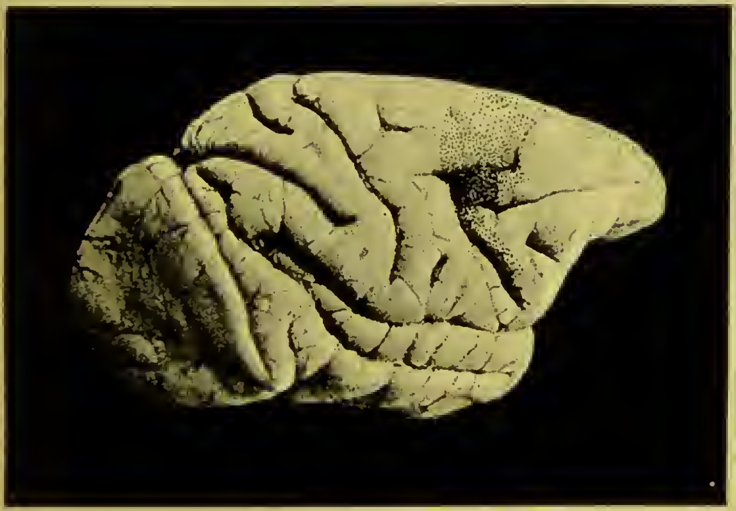


Fig. 5.—PRIMARY REPRESENTATION OF THE SIMULTANEOUS ROTATION OF THE HEAD AND EYES.

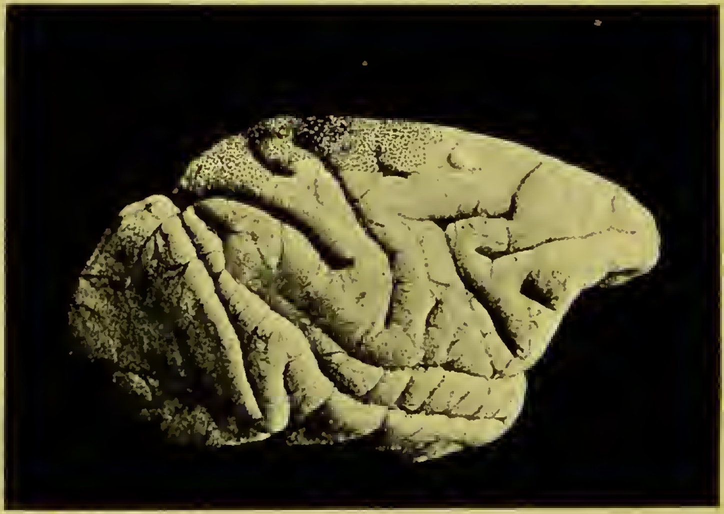


Fig. 6.—ABSOLUTE REPRESENTATION OF THE HALLUX.

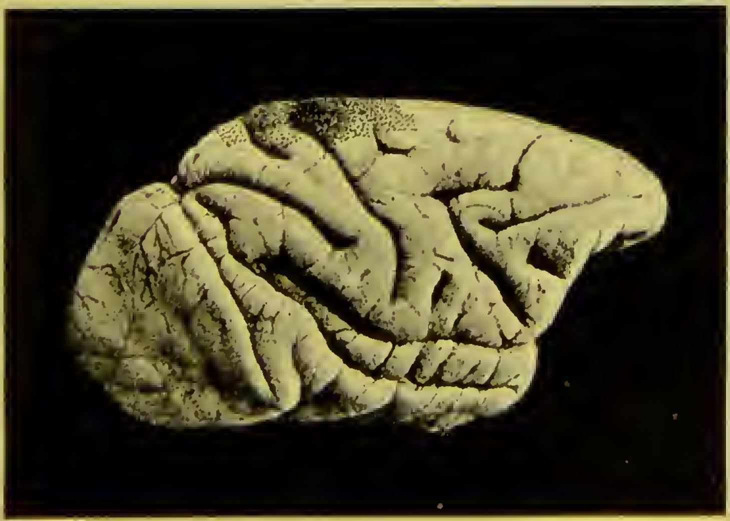


Fig. 6*a.*—PRIMARY REPRESENTATION OF THE HALLUX.

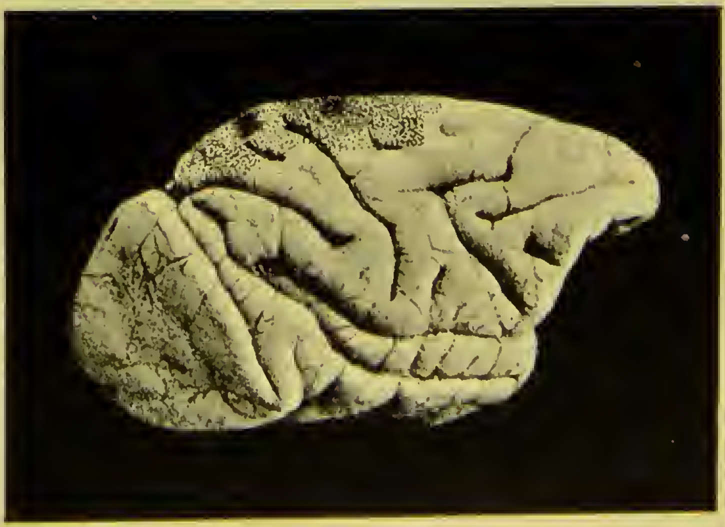


Fig. 7.—ABSOLUTE REPRESENTATION OF ALL TOES.

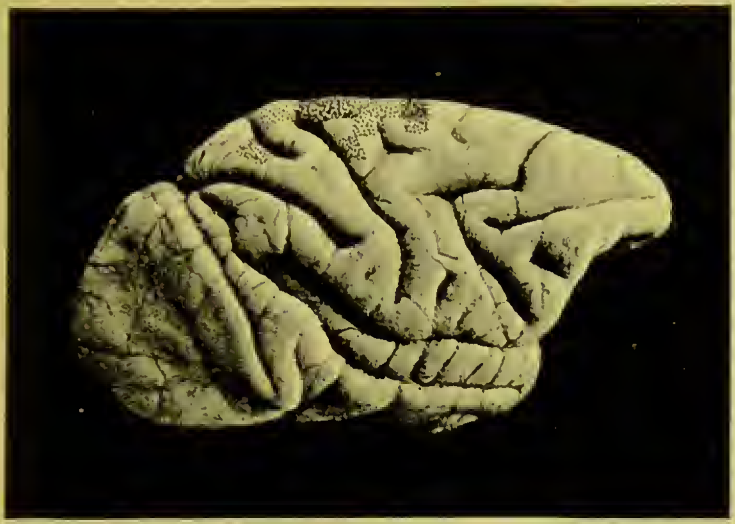


Fig. 8.—Representation of the movement of Flexion of All Toes.

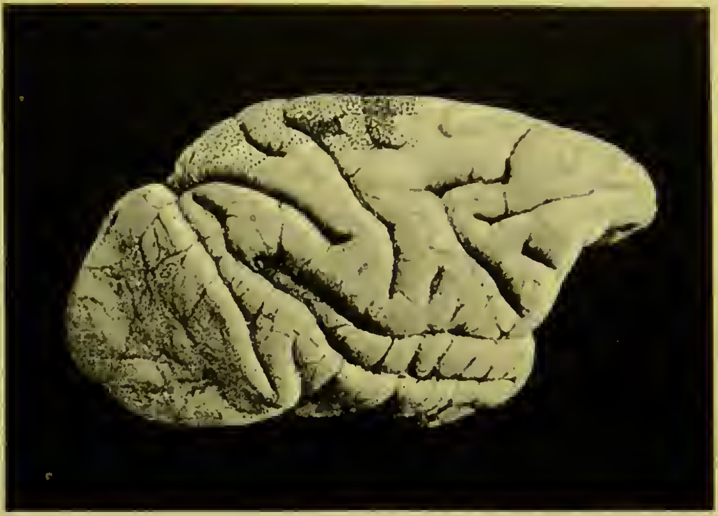


Fig. 9.—Absolute representation of the Small Toes.

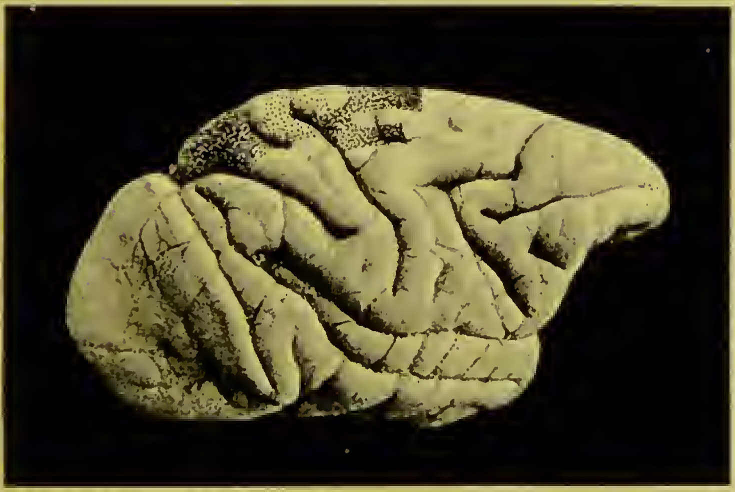


Fig. 10.—Primary representation of the Small Toes.

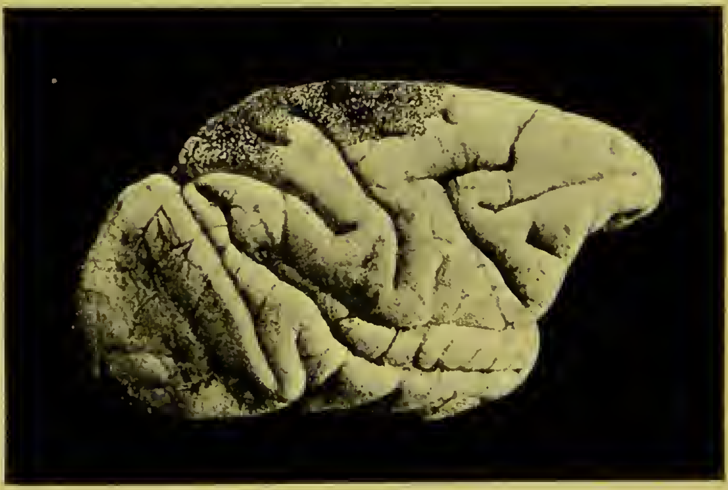


Fig. 11.—Absolute representation of the Ankle.

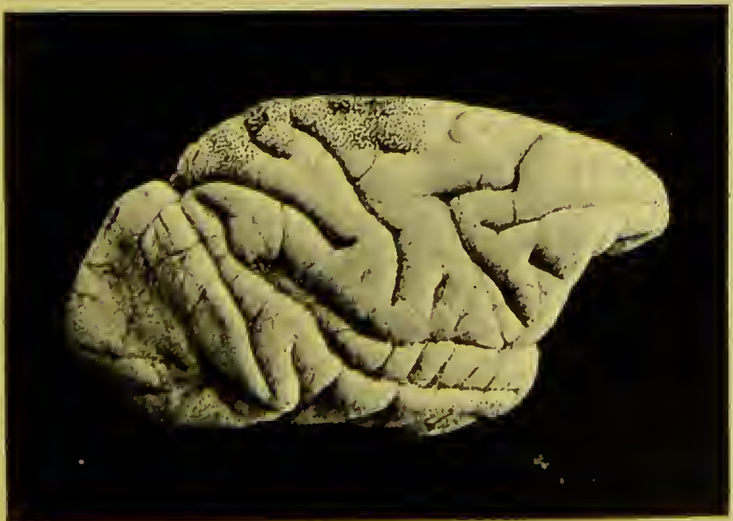


Fig. 12.—Absolute representation of the Knee.

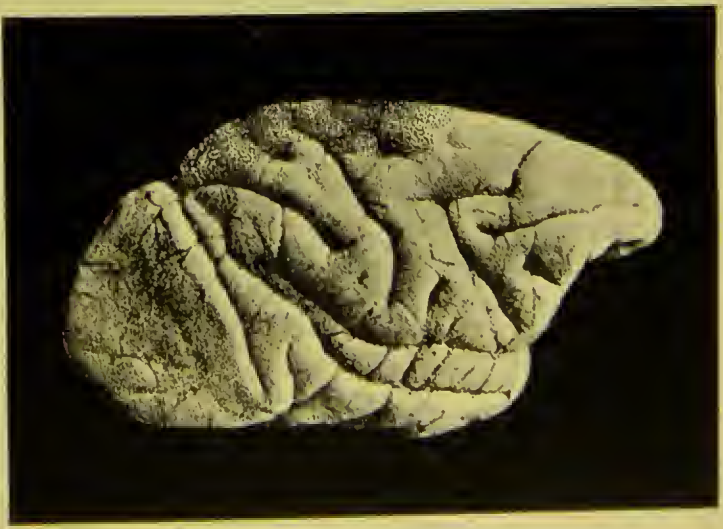


Fig. 13.—Absolute representation of the Hip.

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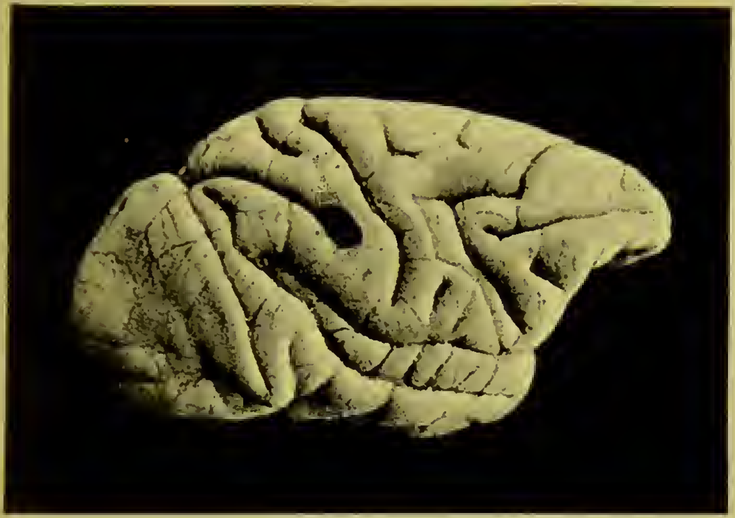

Fig. 16.—ABSOLUTE REPRESENTATION OF THE THUMB.

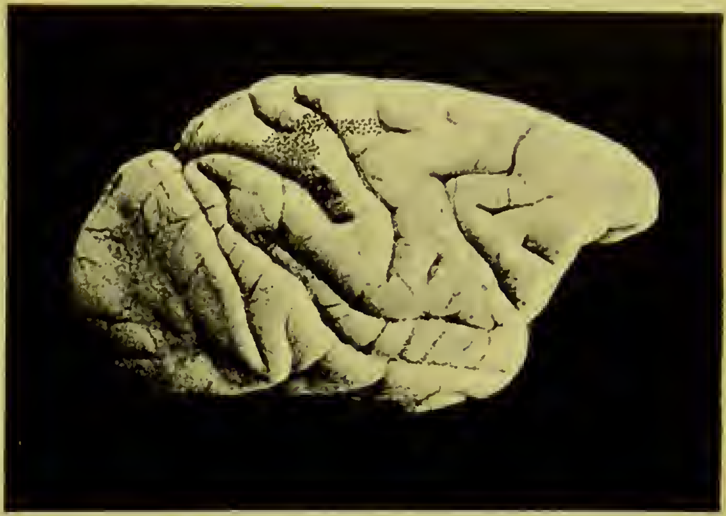

Fig. 17.—ABSOLUTE REPRESENTATION OF THE FINGERS.

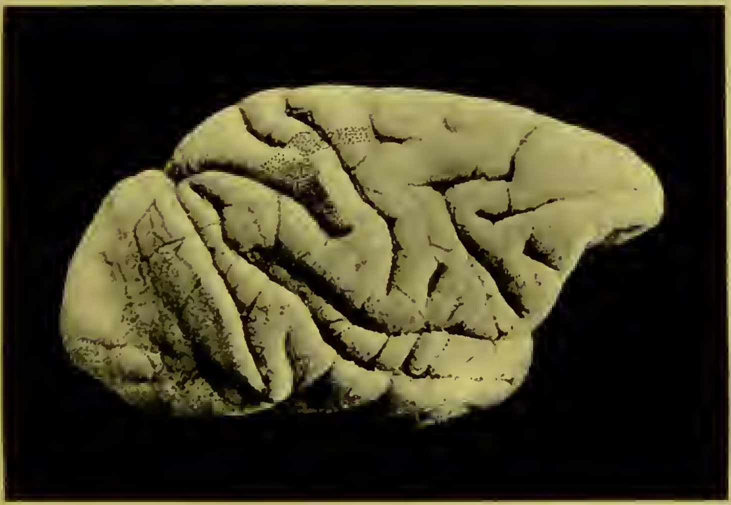

Fig. 18.—ABSOLUTE REPRESENTATION OF THE WRIST.

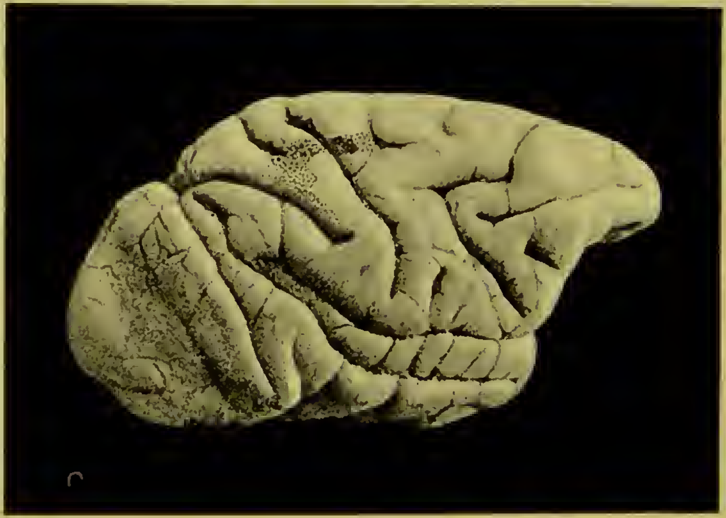

Fig. 19.—ABSOLUTE REPRESENTATION OF THE ELBOW.

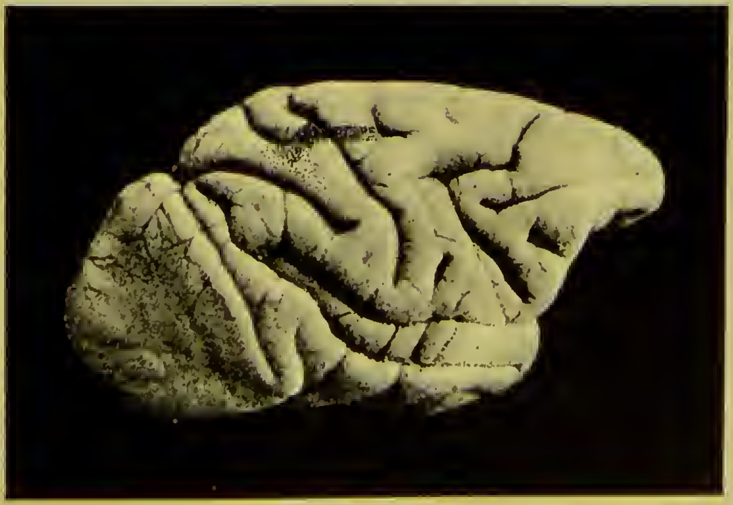

Fig. 20.—ABSOLUTE REPRESENTATION OF THE SHOULDER.

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III. *An Experimental Investigation into the Arrangement of the Excitable Fibres of the Internal Capsule of the Bonnet Monkey* (Macacus Sinicus).*

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(*From the Laboratory of the Brown Institution.*)

Received Dec. 4,—Read Dec. 12, 1889.

[Plates 5–11.]

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Introduction.

In the following paper we propose to give the results of a research on which we have been engaged nearly three years, and by which we hoped to elucidate the arrangement of the motor fibres in the internal capsule.

The fibres which connect the excitable areas in the cortex cerebri with the bulbo-spinal grey matter in the medulla oblongata and spinal cord are commonly spoken of as forming the *pyramidal tract.*

These fibres course downwards between the caudate and lenticular portions of the corpus striatum and the optic thalamus. In passing through this region they enter into the composition of the bundles of white fibres, which received from the older anatomists the unfortunately misleading title of the *internal capsule.* It is obvious

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* The expenses of this investigation have been defrayed by a grant partly from the Royal Society, and partly from the British Medical Association.

that, when the destination and function of these fibres is fully known, this term will be abandoned with great advantage for a specific topographical nomenclature. At present, however, we must use the old expression in default of a better one.

In previous investigations ('Phil. Trans., B., 1887, 1888) we have described the foci* of representation in the cortex cerebri of the Macacque Monkey (*Macacus sinicus*), of the movements of the chief divisions of the body.

It remained for us to see whether there were issuing from such foci bundles of fibres conveying the functional impulses originating in those foci, and whether such fibres were arranged, as has been suggested by one of us ('Lancet,' July, 1884), in an order similar to that which prevails on the surface of the cortex.

From what has been already done in this matter it is evident that the problem can be attacked in two different ways, either by stimulation of the motor fibres of the internal capsule, or by removing different parts of the so-called motor cortex, and tracing downwards the degeneration produced in the motor fibres through the internal capsule and crus cerebri.

In this present paper, we have employed only the former of these two methods, viz., electrical stimulation of the fibres of the internal capsule, as exposed in horizontal section of the hemisphere. Some knowledge of the arrangement of the fibres in the internal capsule has already been gained by experimental and anatomical research, and the facts as known at the present time we will now summarise.

HISTORICAL INTRODUCTION.

Previous writers, on this question, have investigated the subject by several methods in different kinds of animals, viz., Rodents, Carnivora, Monkeys, and Man. The methods employed were for the most part anatomical, or consisted in tracing paths of degeneration. Very rarely has excitation been resorted to. Considering the varied mode in which movement is represented in the cortex of the brain in different animals, we have thought it best to arrange the facts we have deduced from the above researches under the headings of the various species of the animal examined, in the order already given.

Birds.

PITRES† found that in Pigeons and Chickens ablation of a hemisphere produced no descending degeneration.

Mammals.

Rodents.

PITRES† found that in the Guinea Pig and Rabbit destruction of the excitable parts of the cortex produced descending degeneration, which cannot be traced beyond the lower limits of the bulb—*i.e.*, beyond the anterior pyramid of the same side.

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* By the term "focus" we mean the point where the movements of any given segment are most intensely represented.

† 'Comptes Rendus de l'Académie des Sciences,' vol. 99, July, 1884. p. 89.

NOTHNAGEL[*] never observed motor paralysis to follow either unilateral or bilateral division of the internal capsule in the Rabbit.

MONAKOW[†] removed in the Rabbit the anterior portion of the hemisphere, including part of the excitable zone, and found that this was followed by atrophy of the anterior part of the internal capsule. Removal of the middle zone of the cortex produced atrophy of the third fifth of the capsule, while destruction of the hinder third of the hemisphere (*i.e.*, occipital portion) caused atrophy of the hinder third of the capsule. He further found[‡] that removal of FERRIER'S centres 6 and 9 produced respectively atrophy of the hinder and dorsal part, and of the posterior part of the capsule. Finally, the corpus striatum was always normal.

GUDDEN[§] figures (fig. 4, Taf. VIII.) a section of the hemisphere of a Rabbit, the upper third of which, including a thin slice of the corpus striatum, had been removed. The specimen shows marked atrophy of the internal capsule. The same author[||] also removed in young Rabbits the frontal lobe ("stirnhirn") and found that while the corpus striatum remained normal, the "medial part of the peduncle" and the corresponding pyramid and spinal cord were atrophied.

Carnivora.

Several authors have made experiments on the Cat and Dog.

J. BURDON-SANDERSON[¶] excited electrically in the Cat the fibres of the corona radiata, and subsequently the corpus striatum, producing the same movements as he had previously obtained by excitation of the cortex.

CARVILLE and DURET.[**] These authors divided the anterior two-thirds of the internal capsule in the Dog, and thus produced hemiplegia. In a second experiment they found that division of the posterior three-fourths produced also hemiplegia, but accompanied by hemianæsthesia.

VULPIAN,[††] having extirpated the right sigmoid gyrus 183 days previously, the right internal capsule was found, *post mortem*, to be "much thinner" than that of the left side.

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[*] 'Archiv für Pathologische Anatomie und Physiologie und für Klinische Medicin,' vol. 71, 1877. p. 280.

[†] "Weitere Mittheilungen über die Extirpation circumscripter Hirnrindenregionen, &c." 'Archiv für Psychiatrie und Nervenkrankheiten,' vol. 12, 1882, p. 535.

[‡] *Loc. cit.*, p. 141.

[§] 'Archiv für Psychiatrie,' &c., vol. 2, 1870, p. 693.

[||] 'Correspondenzblatt für Schweizer Aertzte,' vol. 2, p. 79.

[¶] Note on the "Excitation of the Surface of the Cerebral Hemispheres by Induced Currents," 'Roy. Soc. Proc.,' vol. 22, p. 368, 1874.

[**] "Sur les Fonctions des Hemisphères Cérébraux," 'Archives de Physiologie, vol. 2, 1875, p. 465.

[††] 'Archives de Physiologie,' vol. 3, 1876, p. 814.

PITRES* found marked descending degeneration in the Dog and Cat, after ablation of the excitable cortex, around the crucial sulcus. The major part of the degeneration ceased at the lower limit of the bulb.

GUDDEN† found that extirpation of the frontal region (stirnhirn) in young Dogs produced atrophy of the "medial part of the peduncle," corresponding pyramid and spinal cord.

LÖWENTHAL‡ found that in the Dog, after removal by Professor HERZEN of the left sigmoid gyrus, some of the lenticulo-striate fibres were atrophied just in front of the genu, and that, of the posterior limb, the fibres composing its anterior third were also atrophied. In a section taken lower down, just above the level of the anterior commissure, the portion of the posterior limb of the internal capsule found to be degenerated proved to be the second and third fifths from before back.

A section through the upper part of the crus showed the inner two-thirds to be degenerated; while in a section lower down—*i.e.*, opposite the exit of the third nerve—the middle third only was degenerated.

FRANCK and PITRES§ obtained, on excitation of the internal capsule in the Dog, the following results:—

Dividing the capsule into motor fasciculi, they found the arrangement from before backwards to be as follows:—

Opening of eyelids and dilatation of pupils;
Movement of opposite fore foot only;
Associated movements of both opposite limbs;
Movement of opposite hind limb only;
Closing eyelids;
Pricking of the opposite ear.

VEYSSIÈRE,|| by a special instrument, produced hemianæsthesia by a lesion of the posterior third of the hinder limb of the internal capsule.

Quadrumana.

SCHÄFER¶ noted the following facts in a Monkey previously operated on by Professors FERRIER and YEO:—

The parts removed were the ascending frontal gyrus, except a small portion at the

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* 'Comptes Rendus de l'Académie des Sciences,' vol. 99, July, 1884, p. 90.

† *Loc. cit.*

‡ "La Région pyramidale de la Capsule Interne chez le Chien, et la Constitution du Cordon antéro-latéral de la Moelle." 'Revue Médicale de la Suisse Romande,' vol. 6, p. 529, Plates VII. and VIII., 1886.

§ 'Leçons sur les Fonctions Motrices du Cerveau,' &c., par FRANCK. Paris, 1887, pp. 21, 22.

|| 'Recherches Cliniques et Expérimentales sur l'Hemianæsthésie de Cause Cérébrale,' 1874.

¶ "Report on the Lesions, Primary and Secondary, in the Brain and Spinal Cord of the Macacque Monkey exhibited by Professors FERRIER and YEO." 'Journ. of Physiology,' vol. 4, Nos. 4 and 5, Dec., 1883, p. 323, Plate XII.

upper end next the longitudinal fissure, and except also its lower end, amounting nearly to one-third of the length of the whole gyrus; also the posterior third of the upper division of the anterior portion of the frontal lobe.

Further, the ascending parietal gyrus was removed, except 5 mm. at the upper and 6 mm. at the lower end, and a small piece of the parietal lobule; and, in addition, rather more than half of the ascending limb of the angular and the supra-marginal gyri.

The effects of this lesion were as follows:—

Internal capsule.—Sections of the internal capsule showed in its "central part" a number of bundles mostly degenerated, which were not all closely packed together, but were somewhat scattered, being here and there separated by others which presented a normal appearance. In many of the flattened degenerated bundles there was a thin layer forming a sort of cortical stratum, in which the fibres appear normal.

In a section of the crus cerebri a patch of degeneration was found to be situated in the central part of the crusta, localised near the ventral border as an oval area tapering mesially.

FERRIER[*] found in the Monkey that removal of the præfrontal regions was followed by degeneration of "the lowermost and most internal" fibres in "the transverse sections of the internal capsule and the most median bundles of the foot of the crus cerebri."

Examination of the photographs of the brains shews that in each case the cortical areas for turning of the head and eyes were encroached upon by the lesion.

Man.

TURCK[†] in his original memoir showed that in cases of long-standing hemiplegia the hinder and upper part of the capsule was degenerated, and also the middle segment of the crus.

FLECHSIG[‡] observed in a new-born infant, 44 cm. long, that the internal capsule was white only between the thalamus and lenticular nucleus. At the same time the laminæ medullares of the lenticular nucleus as well as the fibres surrounding their posterior extremities were brighter than the neighbouring parts. In the crus cerebri there was seen on the lower and outer side a sharply bounded bright band 3 mm. broad (pyramidal tract) which was continued up into the internal capsule close to the innermost zone of the lenticular nucleus. In a further paper[§] he shows reason for believing that in a horizontal section through the upper border of the middle zone of the lenticular nucleus, the pyramidal tract, including the fibres to the seventh and twelfth nerves, occupies the second, third, and fourth sixths of the posterior limb of the internal capsule.

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[*] "A record of experiments on the effects of Lesion of different regions of the Cerebral Hemispheres," with GERALD YEO, 'Phil. Trans.,' 1884.—Experiments 22 and 23, p. 528.

[†] 'Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften,' vol. 6, Wien, 1851, p. 300.

[‡] 'Die Leitungsbahnen im Gehirn und Rückenmark des Menschen,' Leipzig, 1876, pp. 27, 28, Taf. II., fig. 3.

[§] 'Archiv für Anat. und Phys. (Anat. Abth.),' 1881, p. 12.

CHARCOT* sub-divided the capsule according to his well-known plan, as follows :—

The anterior limb he termed the lenticulo-striate bundle. The posterior limb he subdivided into thirds, the two anterior of which he regarded as belonging to the pyramidal tract, while the remaining third was, he believed, limited to the transmission of afferent impressions.

We may remark that, as will subsequently be seen, this description applies only to one sectional level of the capsule.

BRISSAUD† made the most numerous clinical observations on this point. According to him there exist in the crus cerebri four bundles, whose relations from behind forwards may be stated as follows :—

1. A posterior bundle for the transmission of sensory impressions (CHARCOT, MEYNERT).

2. A middle bundle for the innervation of the muscles of the limbs and trunk.

3. A bundle of small size, which he called the geniculate bundle on account of its connection with the genu of the internal capsule. This bundle includes motor fibres, and is distributed to the bulbar nuclei for the movements of the muscles of the face, the tongue (perhaps the soft palate) ; in fact to all parts of the head and face which can be acted on voluntarily.

4. An internal bundle which ends in like manner in the bulb, and whose degeneration only seems to be coincident with intellectual derangements.

To these four bundles the four following divisions of the internal capsule correspond.

1. To the posterior bundle, the posterior third of the hinder limb corresponds (*i.e.*, the region of hemianæsthesia, CHARCOT, RAYMOND).

2. To the middle bundle, the anterior two-thirds of the hinder limb.

3. The bundle which he called geniculate, corresponds to the genu of the capsule.

4. Finally the whole of the anterior limb of the internal capsule corresponds to the internal bundle of the crus.

Contrary to what certain authors have stated, the crus cerebri cannot become completely degenerated ; in other words there is a limit which the degeneration cannot overstep.

This maximum degeneration is recorded by him in observation VII., where the degeneration affected the internal three-fourths of the lower level, and only the posterior fourth escaped. In this case all the frontal lobe, the whole of the parietal lobe and a great part of the occipito-sphenoidal lobe had been destroyed by an extensive superficial softening.

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* 'Leçons sur les Localisations dans les Maladies du Cerveau et de la Moëlle Épinière,' 1876–1880, pp. 221–224.

† 'Recherches sur la Contracture Permanente des Hemiplégiques,' Paris, 1880, p. 38.

Meynert[*] divides the internal capsule into five different kinds of bundles, viz. :—

1. Fibres passing from the cortex, as laminæ medullares, between the zones of the lenticular nucleus.
2. A bundle passing from the frontal region to the optic thalamus, and also forming part of the stratum zonale.
3. Fibres from the nucleus caudatus to the crus cerebri.
4. Fibres from the nucleus lenticularis to crus cerebri.
5. A group of fibres (the most posterior) which pass to the tegmentum.

Hughes Bennett[†] and Campbell published a remarkable case in which the left arm was completely paralysed by a hæmorrhage in the internal capsule.

The lesion was found post-mortem and located as nearly as possible to the junction of the most anterior and second fourth of the posterior limb.

Dejérine[‡] reported a case in which a tubercular tumour of the size of a nut, "seated on the internal capsule, between the posterior part of the optic thalamus and the capsule itself," produced paralysis of the right upper limb, together with incomplete right hemianæsthesia.

Obersteiner[§] figures an arrangement of the fibres of the capsule and crus similar to that given by Brissaud and Charcot.

Wernicke[||] states that the anterior limb of the internal capsule is composed of fibres, which pass partly into the subthalamic region, and partly into the mesial side of the crus, and that the fibres coming from the nucleus caudatus pass circuitously through the laminæ medullares round the two inner zones of the lenticular nucleus.

Anatomy of the Internal Capsule.

Definition of the term.—As before said the term *internal capsule* has been given to the descending and ascending fibres of the *corona radiata,* while passing between the basal ganglia ; consequently we assume that the term is only applicable to the fibres so long as they are passing between the two following levels.

The upper of these levels is shown in Plate 11, fig. 2, which is constructed from a photograph of a transverse vertical section of a Monkey's (*Macacus sinicus*) right hemisphere. This superior level (black dotted line) is seen to be a plane directed slightly obliquely downwards and outwards, and resting on the upper surfaces of the caudate and lenticular nuclei.

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[*] 'Psychiatrie,' Wien, 1884, p. 77.

[†] "Case of Brachial Monoplegia due to Lesion of the Internal Capsule," 'Brain,' vol. 8, p. 78, April, 1885.

[‡] Quoted in article "Encéphale," 'Dictionnaire des Sciences Médicales,' 1887.

[§] 'Anleitung beim Studium des Baues der Nervösen Centralorgane im gesunden und kranken Zustande,' 1888, p. 255.

[||] 'Lehrbuch von den Gehirnkranheiten,' Cassel, 1881, vol. 1, p. 85, fig. 44.

The lower level is scarcely a plane, owing to the configuration of the basal ganglia, as about to be described, but its general direction is roughly represented by a plane inclined upwards and backwards in a line with the upper surface of the optic tract and drawn from the optic chiasma backwards and upwards to the posterior extremity, or the pulvinar, of the optic thalamus.

Of course these levels are purely arbitrary divisions of the fibres of the pyramidal tract, separating a part of them from the centrum ovale above and the crus cerebri below.

The internal capsule may be described as consisting of bundles of fibres, arranged like the rays of a fan, of which the handle if broadened would represent the crus cerebri, while if the fan be considered to be held laterally in a plane parallel to the sagittal section of the hemisphere, the outside rays would correspond respectively with what we shall hereafter term the antero-inferior and postero-superior borders of the internal capsule, this is represented in fig. 3, which is a photograph of a sagittal section of a Monkey's brain (*Macacus sinicus*).

Viewed in horizontal section the capsule is limited by lines drawn at right angles to the anterior and posterior extremities of the lenticular nucleus.

Although this view of the fibres composing the internal capsule is useful to bear in mind, it nevertheless does not express the whole facts of the case. In the first place we have to remember that extending down towards the base of the brain, *i.e.*, towards the basal ganglia and internal capsule, is a large number of fibres converging from all parts of the cortex mantle.

Arranged in order from before back, these fibres may be enumerated as follows, irrespective of the impulses which they are generally considered to convey, classified according to the region of the cortex with which they are apparently connected.

I. Præfrontal.
II. Excitable, Pyramidal, or Fronto-Parietal.
III. Temporal.
IV. Occipito-Temporal.
V. Occipital.

These fibres are shown in their relation to the basal ganglia, anterior commissure, &c., in the accompanying figs. 4, 5, 6. These are drawn from a dissection of a hardened Monkey's (*M. sinicus*) brain in which the large majority of the hemisphere has been cut away, leaving uninjured the nuclei of the corpus striatum. In fig. 4 the ventricular aspect of the mass thus obtained, and also in fig. 6, is seen a dotted line in front, showing how much of the grey matter forming the anterior perforated spot, and part of the amygdaloid nucleus had to be cut away to reveal the anterior commissure (*a.c.*) running under the corpus striatum.

The convergence of the fibres of the capsule is seen in fig. 6, in which the whole of the corona radiata, outer capsule and claustrum, have been removed. It shows the caudate nucleus terminating posteriorly in the surcingle, which ends in the grey matter under the lenticular nucleus.

It is clear that these fibres, when they approach the basal ganglia, either end in these ganglia or pass between them to and from the mesencephalon.

(1) Do any of the fibres descending from the cortex end in the basal ganglia ?

This is a question which will recur, and as its elucidation does not immediately concern us in considering the present point, it may be postponed, see pp. 68, 72.

(2) Do the fibres pass between the basal ganglia to the mesencephalon, and if so which of the classes above enumerated ?

The answer to this question is easier. In the first place the important fibres known as the pyramidal tract pass downwards from the cortex, through the internal capsule into the crus and to the pyramidal region of the mesencephalon. These fibres are universally recognised to be the efferent or motor fibres of the cortex system, and it is the result of the excitation of these fibres which forms the subject of the present communication. In order to make the arrangement of these fibres—as we believe them to exist—more intelligible, we must first refer to the præfrontal class.

I. *Præfrontal.*—The fibres coming from the præfrontal region unquestionably appear in the anterior limb of the internal capsule as horizontal bundles, and compose its antero-inferior border.

Excitation of the præfrontal region of the cortex, as is well-known, has produced no muscular movement except in the hands of MUNK.* Ablation of the same region has been stated by Professor FERRIER † to have been followed by descending degeneration in the fibres of the anterior limb of the internal capsule. His results, however, judging from the figures he gives of the brains thus operated upon, seem to have included portions of the excitable area for the representation of the movements of the head and eyes.

Anatomical investigation goes to show that the fibres of the anterior limb of the capsule pass to the mesial side of the crus and also to the subthalamic region. Of such fibres our method gave only negative evidence, since in Groups III., VI., VII. (see fig. 1) the anterior limb was practically inexcitable, it is therefore clear that these præfrontal fibres at any rate do not possess efferent motor function.

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* MUNK, "Ueber die Stirnlappen des Grosshirns;" 'Sitzungsberichte der k. Preussischen Akademie,' 1882.

† 'Functions of the Brain,' 2nd edition, pp. 398, 399.

Whatever be their function it is evident that the fibres entering the anterior limb are arranged much as is indicated in fig. 3, and that, regarding the hemisphere as fixed with its greatest length in a horizontal plane, we may group these fibres, according to their vertical relations to such a plane, into :—

a. Superior and Descending.
b. Horizontal.
c. Inferior and Ascending. See also figs. 3, 5, 6.

But further, on account of the manner in which the grey cortical mantle of the frontal lobe presents, roughly speaking, the form of a cap or segment of a globe, we must, in addition, sub-divide these fibres according to their relative position about the horizontal plane of the hemisphere. Hence we must speak of a middle bundle, viz., those from the tip and anterior part of the lobe; of an internal group, viz., those coming from the mesial surface, *i.e.*, of the anterior third of the marginal and neighbouring gyri; and of an external group, *i.e.*, those coming from the outer part of lower frontal gyri (of course excitable).

Many of these bundles will be referred to under the next heading, and the destination of the remainder, *i.e.*, of the truly præfrontal, we have already discussed.

To sum up then, it is evident that we have excitable fibres coming into the anterior limb from the so-called motor cortex lying on the external aspect of the hemisphere in the opercular region, and these we regard as motor. The mass, however, of the anterior limb is composed of the bundles of fibres coming from the most anterior and mesial surfaces of the frontal lobe, these being non-excitable.

Looked at in their sagittal arrangement, we find that the excitability diminishes from above down, or, in other words, the pyramidal portion decreases and the præfrontal and non-excitable increases.

II. *Excitable or Pyramidal, Fronto-Parietal.*—This is the collection of fibres commonly known as the pyramidal tract, and which on being stimulated produce movement in a distinctive manner. Strictly speaking, the term pyramidal tract should apply only to those fibres contained in the pyramids, *i.e.*, those for the muscles of the limbs and trunk. In fact, many authors divide the "motor" capsular fibres into two groups, one devoted to the cerebral nerves, and the other termed the pyramidal fibres. This distinction we consider fair, but the term pyramidal tract has been so extended as to include these two groups of so-called motor fibres. But, while we agree in general to this distinction, it must not be forgotten that these two sets of fibres are not in utterly distinct compartments, but that the area of each overlaps.

We would prefer, therefore, to employ the term excitable to express the whole number of fibres possessing "efferent" or "motor" function.

These fibres we presume come from most of the excitable portions of the cortex.

We say *most* of the excitable region, because the recent investigations of SCHÄFER* show that on excitation of the occipital and angular gyri certain movements of the eyes are evoked, which, by reason of their greater latency of production, seem to be a result of secondary stimulation of the area for such movements situated in the frontal region.† Consequently, although this point is still greatly *sub judice,* it seems probable that the excitable fibres of the internal capsule only come from the fronto-parietal region. The course they take to reach the various points in the capsule will be determined by the anatomical relations of the cortical mantle to the basal ganglia, the exact lines of such courses, though not yet determined anatomically, may be theoretically imagined.

We have ascertained the anterior and posterior limits respectively of the excitable fibres in each experiment, and have constructed the following outlines, see fig. 1 (twice the natural size), showing the delimitation of these fibres in each group, the position of each point being determined by the averages given in Table I., see next page.

III., IV., V. *The Temporal, Occipito-Temporal, and Occipital Fibres.*—The delimitation of these fibres we have only in the present research ascertained by the process of exclusion, *i.e.*, by their non-excitability. We believe that they have for the most part to do with the general and special senses, but the method of the present research does not throw any fresh light on the subject.

It is, however, worthy of note that even in the narcotised state, when the scalpel divided these fibres at the hinder end of the capsule, there frequently occurred a marked general reflex movement. Excitation of the peripheral ends of these cut fibres produced, of course, no effect.

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* 'Roy. Soc. Proc.,' vol. 43, 1888, p. 411.

† *Cf.* also SHERRINGTON's very valuable anatomical confirmation of SCHÄFER's statements. 'Proceedings of the Physiological Society,' March, 1889.

TABLE I.*

Group I.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Tongue protruded	7	..	24	15
Mouth opens	13	..	51	32
Eyes turn	22	..	60	41
Opening eyes	24	..	55	39
Head and eyes turn (simultaneously)	41	..	54	47
Head turns	42	..	50	64
Retract angle of mouth	58	..	64	82
Shoulder	61	..	71	66
Elbow	62	..	87	74
Fingers	67	..	80	73
Abdomen	70	..	88	79
Wrist	75	..	81	78
Thumb	76	..	83	79
Hip	76	..	94	85
Small toes	78	81	98	88
Hallux	80	..	96	88
Knee	81	..	93	87
Ankle	86	..	95	90

Length of capsule, 100.

Group II.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Eyes turn	25	50	68	47
Opening eyes	37	..	61	49
Head turns	42	62	71	56
Mouth opens	43	..	57	..
Retract angle of mouth	48	55	83	65
Shoulder	55	..	88	71
Tongue protruded	57	..	61	59
Fingers	58	75	86	72
Elbow	58	81	87	72
Wrist	60	..	71	65
Abdomen	60	..	80	70
Thumb	73	81	90	81
Hip	75	..	86	80
Knee	79	..	85	82
Small toes	82	88	91	86
Ankle	84	..	96	90
Head and eyes turn	..	84	..	84
Hallux	92	93	100	96

Length of capsule, 100.

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* See also p. 71.

Group III.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Opening eyes	41	54	62	50
Eyes turn	48	49	60	54
Head and eyes turn (simultaneously)	53	. .	60	56
Head turns	56	. .	70	63
Mouth opens	57	. .	71	64
Retract angle of mouth	58	71	79	68
Tongue protruded	62	. .	72	67
Elbow	66	73	88	77
Thumb	69	. .	84	77
Fingers	69	73	84	77
Shoulder	69	70	84	77
Wrist	70	74	88	79
Hip	79	. .	84	82
Abdomen	80	. .	86	83
Knee	80	. .	86	83
Ankle	83	. .	89	86
Hallux	84	. .	91	87
Small toes	85	. .	91	87

Length of Capsule, 100.

Group IV.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Eyes turn	23	. .	57	40
Opening eyes	30	45	60	45
Head turns	34	55	65	55
Mouth opens	40	. .	62	51
Shoulder	50	. .	65	57
Retract angle of mouth	50	65	85	65
Fingers	52	. .	80	66
Head and eyes turn (simultaneously)	55	. .	. .	55
Wrist	55	. .	75	65
Elbow	55	. .	80	67
Tongue	55	. .	82	72
Thumb	62	. .	82	72
Ankle	72	. .	85	78
Abdomen	75	. .	85	80
Hip	75	. .	85	80
Knee	75	. .	85	80
Small toes	75	. .	90	82
Hallux	75	. .	90	82

Length of Capsule, 100.

Group V.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Eyes open	38	47	54	46
Eyes turn	38	48	59	48
Head turns	41	..	58	49
Mouth opens	44	..	48	46
Head and eyes turn (simultaneously)	53	..	60	56
Angle of mouth retracted	54	76	80	67
Tongue protruded	55	..	76	65
Elbow	57	..	82	69
Fingers	57	..	84	70
Shoulder	58	..	81	69
Abdomen	58	66	85	71
Wrist	62	80	82	72
Thumb	64	..	79	71
Hip	68	..	80	74
Knee	74	..	77	75
Hallux	77	..	84	80
Small toes	79	..	85	82
Ankle	80	..	88	84

Length of capsule, 100.

Group VI.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Eyes open	40	..	64	52
Eyes turn	42	..	60	51
Head turns	47	61	66	56
Elbow	48	..	75	61
Angle of mouth retracted	51	..	78	64
Tongue protruded	55	..	..	55
Mouth open	55	..	63	59
Shoulder	57	..	69	63
Fingers	59	..	77	68
Thumb	60	..	72	66
Wrist	62	..	72	67
Hip	69	..	77	73
Ankle	71	72	82	79
Knee	76	..	82	79
Abdomen	77	..	83	80
Small toes	78	..	82	80
Hallux	78	..	82	80

Length of capsule, 100.

Group VII.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Eyes open	5	..	51	28
Eyes turn	5	..	51	28
Head turns	22	..	45	33
Head and eyes turn	29	..	35	32
Tongue protruded	35	..	52	43
Abdomen	41	52	58	49
Angle of mouth retracted	45	55	65	55
Shoulder	45	..	65	55
Wrist	48	..	62	55
Elbow	51	..	65	58
Thumb	55	..	61	58
Hip	56	.	65	60
Fingers	57	..	62	59
Hallux	61	..	72	66
Ankle	64	..	..	64
Knee	66	..	..	66
Small toes	66	..	72	69

Length of capsule, 100.

Group VIII.

Character of movement.	Anterior limit.	Point of observed maximal intensity.	Posterior limit.	Average.
Eyes turn	8	.	41	24
Eyes open	16	..	41	28
Angle of mouth retracted	16	28	50	33
Elbow	16	41	62	39
Shoulder	20	58	66	43
Head turns	33	41	66	48
Fingers	37	..	62	49
Wrist	41	..	62	51
Small toes	49	..	66	57
Ankle	49	..	75	62
Abdomen	50	..	..	50
Hallux	53	..	66	59
Thumb	48	..	66	62

Length of capsule, 100.

The Configuration of the Basal Ganglia.

It is now necessary to consider in detail the shapes and relative positions of the three chief divisions of basal grey matter, to the fibres of the internal capsule.

We think we may best accomplish this by describing in succession from above down the sections typical of each group of experiments (see p. 65). The position of the genu, which, as will be seen in fig. 1, gradually moves backwards and inwards, as we pass down the capsule to near the base, *i.e.*, until the posterior limb, as seen in these sections, changes from an oblique antero-posterior direction to an almost transverse position. This is strikingly exhibited in Table II., calculated from the observed dimensions of the capsule in each experiment.

TABLE II.

Group.	Average total length of capsule.	Length of Anterior Limb.	Length of Posterior Limb.
	m.m.	m.m.	m.m.
I.	18·2	7	11·2
II.	17	6	11
III.	18	7	11
IV.	20	9	11
V.	21	10	11
VI.	20	9	11
VII.	17	2	15
VIII.	12	0	12

The genu is of course the point of junction of the two limbs, and it will be seen at once that while the length of the posterior limb remains remarkably constant until its axis finally changes direction, the anterior limb on the other hand increases in size from above down, lying in the notch between the caudate and lenticular nuclei (see figs. 1, 2, and 5), until the section approaching the grey matter of the base of the brain, it rapidly disappears (as in Group VIII.), see fig. 1.

It will be convenient next to consider two angles; firstly that which the anterior limb makes with the posterior limb in forming the genu, and secondly the angle of inclination of the long axis of the posterior limb to the middle line. By subtraction of these two from 180° we naturally obtain at once the inclination of the anterior limb to the mesial plane.

Since the angle of the genu is correlated with that of the inclination of the anterior limb, we set both out in the following Table III. (The angles we measured with a goniometer on photographs of the specimens made just after each experiment.)

Each of the angles typical of the several groups was found by taking the average of all the angles of the capsules contained in each group.

TABLE III.

Group.	Angle of genu.	Angle of inclination of axis of posterior limb to mesial line.	Angle of inclination of axis of anterior limb to mesial line.
	°	°	°
I.	134·5	15·8	29·7
II.	123·3	20·3	36·4
III.	118·9	30·8	30·3
IV.	105·1	36·2	38·7
V.	97·1	44·8	38·1
VI.	87·9	55	37·1
VII.	Not ascertainable	40*	..
VIII.	No genu	57·5	..

From this Table it is clear how, while the posterior limb is constantly altering its inclination to the mesial plane, the anterior limb moves comparatively slightly from the same plane in the middle three-fifths of the depth of the capsule. In other words, the caudate wall of the groove separating the anterior ends of the striate nuclei is practically vertical, though slanting outwards rapidly above, more slowly below, as is seen to be the case, when a frontal section is made of the anterior limb. (See fig. 2.)

It is necessary now to give what we have regarded as the defining points of difference between the several groups of capsules experimented on. (See fig. 1.)

Group I. (the highest).—Genu forms a widely open angle (134·5°) so that the capsule is almost a segment of a circle. Of the lenticular nucleus only the outer zone or putamen appears, and it has a bi-convex outline. (See typical photograph, Plate 10, Experiment 35 of our series, and fig. 1.)

Group II.—The genu is distinct and less obtuse, being 123·3°. The second zone of the lenticular nucleus has not yet appeared, though the caudate reaches backward to a point a little posterior to the genu (the anterior part of the surcingle). (See typical photograph, Experiment 67.)

The outline of the lenticular is now becoming triangular.

Group III.—The angle of the genu is becoming still smaller, averaging 118·9°. The second zone of the lenticular nucleus is not yet visible though nearly exposed. The caudate nucleus reaches posteriorly to the genu. The lenticular nucleus is becoming more triangular. In the large majority of sections the pulvinar is evidently free in the ventricle. (See typical photograph, Experiment 42.)

Group IV.—This group is easily marked, since in it we have with the main features given under Group III., the first appearance of the second or middle zone of the lenticular nucleus. (See typical photograph, Experiment 31.)

Group V.—The second zone is more marked, the white interzonal or lamellar fibres separating this zone from the putamen are in this section extended backwards almost to the end of the lenticular nucleus. The angle of the genu is nearly a right angle, and the limbs of the capsule are approximately equal in length. (See typical photograph, Experiment 69.)

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* Probably this figure is unexpectedly low, owing to (1) the crescentic shape of the capsule, (2) the number of observations being few, viz., two.

Group VI.—This group is the same as Group V., from which, as the individual capsules show, it can only be separated by the smaller angle of the genu and by the axis of the posterior limb, becoming more transverse to the longitudinal axis of the hemisphere. (See typical photograph, Experiment 50.)

Group VII.—This group is very definite since it shows sections of all three zones of the lenticular nucleus, and since the level is below the capsular groove between the two nuclei in the corpus striatum, it passes through the basal grey matter of the floor of the lateral ventricle. The anterior commissure appears near the middle line; the part seen corresponds to the highest point of the arch it forms. Since this section is cut along the line of the Fissure of SYLVIUS, it necessarily is wholly below the frontal lobes. As will be seen, there is a slight anterior limb in this section, see fig. 1. (See typical photograph, Plate 11, Experiment 81.)

Group VIII.—This section just above the crus closely resembles Group VII., save that the anterior limb is no longer represented, and the two innermost zones of the lenticular nucleus cannot now be separated. (See typical photograph, Experiment 79.)

Notes on Groups VII. and VIII.—In these groups the basal ganglia and capsule, as divided by these sections, present a very constant figure; thus the posterior limb of the internal capsule makes an angle with the middle line of about 60°, its posterior border being formed by the optic thalamus, while anteriorly there are ranged along its front the respective ends of the three grey zones of the lenticular nucleus. If the section pass just above the Fissure of SYLVIUS the three zones will be seen, if lower, the two innermost zones are found to be confused into one grey mass and cannot be separated.

In the *highest sections* (*i.e.*, those in which the three zones are distinct) of these groups, there are the remains of the anterior limb of the capsule lying to the inner side of the innermost zone of the lenticular nucleus. This remnant of the anterior limb is (in the highest sections), about 3 mm. long in the antero-posterior direction. This bundle of white fibres is not in immediate contact with the anterior commissure, but is separated from it by some of the grey matter of the lenticular nucleus. This delimitation of what we consequently call the anterior limb can be easily seen, and it is from this point that in this group of sections we have commenced the measurement of the capsule, continuing the same as before along its outer margin, *i.e.*, contiguous to the lenticular nucleus, as far as the hinder end of the outer zone of that nucleus (see fig. 1).

The remnant of the anterior limb above described is bounded on its inner aspect, *i.e.*, along the middle line of the cerebrum by a narrow (1–2 mm. wide) strip of inexcitable tissue. (? Septum lucidum and anterior perforated spot, grey matter.)

Summary and Application of the Anatomical Facts.

It remains to connect these anatomical data with the facts observed upon excitation.

In the first place discrimination must be made between the effects of exciting fibres in their continuity and on their transverse section respectively, since it is plain that the identity of result might otherwise lead to an undesirably extended view of the limits of the efferent tract.

Reference to fig. 1 and to Table I. shows that some of the efferent excitable fibres which partly compose the anterior limb in Group I. are rapidly concentrated in the posterior limb as we descend to Group III. These fibres are those for the movements of opening the mouth and protrusion of the tongue, as is shown by a glance at fig. 1, C and F.

At Group IV., fig. 1, it is evident that a further change now occurs Apparently owing to the appearance of the second or middle zone of the lenticular nucleus, that part of the anterior limb which is opposite this second zone is found to be excitable, whereas the rest, which really exactly corresponds with the whole anterior limb of Group III., is inexcitable as in that Group.

It is to be observed (fig. 1) that this excitability of the posterior part of the anterior limb again diminishes until we arrive at Group VII., where, upon the further appearance of the third or innermost zone, the hinder end of this limb is seen to be excitable.

To speak next of the inexcitable fibres of the anterior limb, we have in the foregoing pages referred to the views of those who have treated the subject, and we only would express our belief that these fibres of the anterior limb are for the most part horizontal, and that they pass backwards through the genu to the thalamic region.

A point of equal interest is the arrangement of excitable and inexcitable fibres in the posterior limb of the capsule.

In Groups I. and II., fig. 1, the posterior limb is excitable in its whole length, but, in Group III., the hindermost part (*i.e.*, for the last $\frac{9}{100}$ths) is inexcitable. This inexcitable portion steadily increases as we pass downwards (see fig. 1), so that in Groups VI., VII., and VIII., the excitable part terminates posteriorly at the hinder limit of the middle zone.

The classical dictum,[*] that the sensory fibres are contained in the posterior *third* of the hinder limb of the capsule only holds good for the lowest levels. The gradual character of the development of this inexcitable (afferent) part of the capsule is interesting by way of contrast with the variable arrangement of the excitable fibres in the anterior limb just discussed.

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[*] CARVILLE and DURET, CHARCOT, *loc. cit.*

Genu.—Hitherto we have only indirectly spoken of the genu and its relation to the surrounding parts. To determine its position exactly at the different levels of the capsule, we first, by means of successive horizontal sections parallel to the longest antero-posterior diameter of the hemisphere, exposed the level of our Group I. We then inserted (vertically) a long needle at right angles to the plane of the section just at the genu immediately in front of the most anterior extremity of the optic thalamus. Each successive horizontal (parallel) section of the hemisphere contained, consequently, the position of the genu as in the highest section (the upper level, Group I.).

From these data we found that the position of the genu in its antero-posterior relations varied extraordinarily little, but that the position of the entering angle of the inner border was gradually transferred to that of the outer border, and, finally, in the last three groups, the puncture revealed the fact that the position of the genu, as seen in the highest section and now projected upon the lowest, had moved about 2 mm. in front of, and outside the angle of the outer border of the capsule, or 4 mm. from its original site. In other words, the genu had moved backwards and inwards, and this change of position was more rapidly developed in the lower than the upper sections.

Of course, the inward and backward direction of the efferent tracts is also seen (especially the former) in frontal sections of the capsule.

Laminæ Medullares.—The white fibres, which in horizontal sections of the hemisphere, appear as lamellæ to separate the zones of the lenticular nucleus, but which, in vertical frontal sections, appear to run into and connect the zones, we have repeatedly excited without any result. We, therefore, are led to conclude that these fibres, whatever be their function, do not belong to the great excitable cortico-efferent system.

OBERSTEINER[*] gives a schematic diagram, in which he figures fibres passing down from the cortex through the laminæ medullares to end in the subthalamic region.

WERNICKE[†] suggests that these interzonular, or lamellary fibres, are in part derived from the nucleus caudatus, and are passing down to the crus.

MEYNERT[‡] believes that such fibres are derived from the cortex rather than from the nucleus caudatus.

METHOD OF INVESTIGATION IN THE PRESENT RESEARCH.

Animal Employed.—The Bonnet Monkey (*Macacus sinicus*), *i.e.*, the smaller variety of that species of Monkey, was the animal which we have invariably used.

In all we have performed 45 experiments, and in every case the animal was completely under the influence of ether, and was killed before it recovered from the anæsthetic.

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[*] *Loc. cit.*, p. 334

[†] *Loc. cit.*

[‡] *Loc. cit.*

With few exceptions the left hemisphere was the one used for the examination, and, as a rule, the cortex had just before been minutely explored. It was found most convenient to remove the vault of the cranium for about 1 cm. to the other side of the middle line, and laterally as low as the zygoma in front, and behind to a corresponding level.

The dura mater was reflected over the area thus exposed, care being taken not to injure the longitudinal sinus; the hemisphere was then drawn towards the middle line so as to allow of the middle cerebral artery being ligatured soon after its origin, this was easily done by passing a fine thread beneath the vessel through the contiguous portions of the orbital and temporo-sphenoidal lobes.

A horizontal incision was then made with a long sharp scalpel through the substance of the hemisphere, from the outer surface towards the middle line, but stopping short 1 or 2 mm. of the mesial plane. In this way section of all arteries, save the branches of the ligatured middle cerebral was avoided, and, hence, hæmorrhage was in a great measure prevented. The only vessel which gave much trouble was the lenticulo-striate artery running vertically through the outer zone of the lenticular nucleus. In the first two experiments, we sought to arrest this hæmorrhage by a fine point of an actual cautery, but we found, to our surprise, that although the area touched was extremely small, yet the cut ends of the fibres of the adjacent internal capsule were so damaged (by the radiant heat of the cautery) as to be inexcitable; moreover, we speedily found that all hæmorrhage could be easily arrested by placing on the bleeding point a small cube of amadou.

When the hæmorrhage had thus been controlled the upper portion of the hemisphere which, as described above, had not been completely separated, but merely raised like the lid of a box, was replaced, and preparations were made for recording the results of the stimulation.

The plan of recording which appeared to us likely to afford the most accurate results, and, at the same time, not to involve so much delay in exposing the capsule as to cause the death of the fibres, was as follows:—

Upon paper, on which fine lines were engraved by an engine with mathematical accuracy so as to cover the surface with squares of 1 mm. side, we drew by means of compasses the exact outline of the basal ganglia as exposed by the section.

In this way we obtained at once the cut surface of the internal capsule correctly projected on paper, divided into squares of 1 mm.; these squares we then numbered from the front of the anterior limb of the capsule to the posterior end of the lenticular nucleus. Finally, we stimulated each of these bundles of fibres thus obtained of 1 square mm. area, and recorded the effect produced.

Mode of Stimulation.—The electrodes used were two fine platinum points, 1 mm. apart, so that the excitation should be exactly limited to each square excited. The exciting current was an interrupted induced current obtained from the secondary coil of a Du Bois Reymond inductorium, supplied by a 1 litre bichromate cell. The distance of the secondary coil from the zero point of completely covering the primary was such as to give a minimal stimulus, and this was usually about 10 cm.

After the experiment was completed the animal was killed by excess of chloroform, the hemisphere removed, washed in salt solution and the surface photographed.

Upon the photograph thus obtained, the numbers representing the different bundles of fibres (1 mm. square) were transferred by compasses from the plan originally drawn on the ruled paper.

Mode of Enumeration and Recording Results.—We have just said that we numbered the millimetre squares of the internal capsule in order from before back; we adopted this plan for the reason that as the anterior limit of the excitable portion of the capsule varies in position, *i.e.*, retreats as the section descends (*cf.* fig. 1.), it was necessary to express the position of the fibres having the same function by some means which should bear an absolute value in relation to the rest of the capsule. By this means we have been enabled to trace the bundles having the same function through their various changes of direction as they pass down through the different sections of the capsule to reach the crus.

Inasmuch as the capsule is divided into millimetre squares by the above method, each figure denoting any bundle of fibres represents at the same time the distance of that bundle from the front end of the anterior limb.

In plotting out the plan of the capsule during an experiment we arranged it so that the more important posterior limb should be drawn parallel to one direction of the rows of squares on the ruled paper; consequently, as the anterior limb forms an obtuse angle with the posterior limb, the squares dividing it were necessarily échelonned. This, however, afforded no real difficulty, and the more so since in the most important sections very little of the anterior limb is excitable. We, therefore, expressed each square or bundle of fibres by a fraction, the numerator of which denoted the distance that it was situated from the anterior end of the capsule, while the denominator gave the total length of the capsule in that particular section; in this wise one fraction, or, in other words, the position of one bundle of fibres in one section, is strictly comparable with that in another section.

In order to bring all the fractions thus obtained together, and to find the average position of the representation of any given movement in each group, we converted all the fractions into decimals to two places. We took two places as adequately accurate, since any error beyond would only amount to $\frac{1}{1000}$th of the length of the capsule, and as this actually amounts, on the average, to not more than ·02 mm., it is a length which is far too small to be considered among the errors of the experimental method.

The decimals thus obtained, denoting the squares indicating the localisation of each movement elicited, were next added together in the several groups, and the average taken.

Since these decimals were taken to two places, each capsule in every group becomes divided into a hundred parts, and if we drop the decimal point, we may regard the figure as a whole number, taking the whole capsule to be 100. For example, the movement of "protrusion of the tongue" was observed in Group II. to occur in two experiments, the length of the capsule being respectively in each case 12 mm. and 17 mm., the average therefore being 14 mm. The movement was observed to follow excitation of the first millimetre in each case, and to end at the third millimetre in the one case and at the fourth in the other. Consequently the movement began at $\frac{1}{12}$th and $\frac{1}{17}$th of the actual length of the respective capsules, and was last obtained at $\frac{3}{12}$ths and $\frac{4}{17}$ths.

On converting these fractions into decimals they become respectively ·08 and ·06 for the anterior limit and ·25 and ·23 for the posterior limit, and on taking the averages of these we obtain ·07 and ·24.

Now that we have the situations of the fibres expressed in terms of the average length of the capsules of each group, we need not keep the decimal point if we regard the capsule as divided into a hundred parts, and then take the figure as a whole number, so that in Table I. the limits of the representation of the protrusion of the tongue become 7 and 24, *i.e.*, $\frac{7}{100}$ and $\frac{24}{100}$.

This mode of treating the figures has this great advantage, that whatever the length of the different capsules may be in any group, we can compare the function of the fibres in similar parts.

At the same time this mode of extending the differentiation of the capsule has this disadvantage, viz., that, although taken absolutely, as is represented by the fraction $\frac{1}{14}$, we obtained the movement from the most anterior millimetre of the capsule, yet in converting $\frac{1}{14}$ into a decimal to two places, we necessarily obtain $\frac{1}{14} = {}$·07, and then, in regarding the capsule for purposes of relative comparison as divided into 100 parts (dropping the decimal point), we thus obtain the figure 7, meaning the first seven-hundredths, as representing the first portion at which the movement occurred.

In fact, in attempting to analyse and to compare the results of each experiment, *i.e.*, the fractions, we found it impossible to employ the method of a common denominator, and therefore selected, at Mr. GOTCH'S suggestion, the two places of decimals. We were obliged to take two places of decimals, since, as a glance at Table I.* shows, one place of decimals would not have given the differentiation we have discovered to exist, though at the same time it was clear to us that two places would so extend our subdivisions of the capsule as to make it difficult to convey the absolute expression of the amount (*i.e.*, extent) of representation.

These averages are set out in the last column in Table I., in which the movements are also arranged in their order from before back.

In Table I. the first column gives the names of the movements observed, and, as just stated, in the order in which they occur from before back. The first column of figures denotes the distance from the anterior extremity of the capsule of the first bundle of fibres, excitation of which produced the movement. The third column gives the most posterior point or bundle of fibres at which the movement of a part could be elicited, so that the distance between the figures in these two columns gives the total or absolute extent of the fibres from which that movement of a part could be obtained.

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* See p. 60.

The intermediate or second column gives, in those cases where it was most marked, the point of maximal representation, *i.e.*, of greatest intensity.

Further, it is seen at once that the distribution of the fibres for any one part is not allocated to one small point in the capsule, but spread over it for a certain distance, so that the overlapping seen on the cortex occurs here, though to a larger extent.

To further elucdiate the arrangement of the fibres and to facilitate future reference, we have constructed a series of diagrams (fig. 1, A–R.) on exactly the same scale as fig. 1 (*i.e.*, twice the natural size), on which we have marked the extent of representation in the different groups of sections of each segment observed. In each figure the shaded part represents the fibres, excitation of which produces movement of the given segment. The limits of these fibres were obtained from the numbers of Table I. As we have already drawn attention in describing fig. 1, we would remark on the extraordinary diminution of the fibres before the successive appearance of the zones of the lenticular nucleus, and the equally striking increase of the fibres when these zones become visible, *e.g.*, Groups IV. and VII.

Good examples of this are to be seen in the diagrams for the turning of the eyes, the small toes and hallux (fig. 1, B, Q, R).

PHYSIOLOGICAL RELATIONS OF THE BASAL GANGLIA TO THE INTERNAL CAPSULE.

Although the ventricular surface of the caudate nucleus has been asserted to be excitable by CARVILLE and DURET,* FERRIER,† and MINOR,‡ we have failed to obtain the slightest movement by exciting the sectional surfaces of either of the basal ganglia. We do not advance these observations as of special value, considering that we removed the ventricular surface, but the contrast between the absence of any result when the ganglia were excited and the marked spasm which immediately followed the application of the electrodes to the capsule is in harmony with the observations of FRANCK and PITRES,§ and with whose general deductions on this point we fully agree.

To finally elucidate this important point, we have also excited the intra-ventricular surfaces of the basal ganglia, but without any positive result.

Consequently on review of the experimental evidence, it seems to us most likely that the basal ganglia are really inexcitable.

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* *Loc. cit.*

† FERRIER, *loc. cit.*, p. 264.

‡ 'Neurologisches Centralblatt,' June, 1883.

§ *Loc. cit.*

Analysis of Results.

On pp. 60–63 we give, in Table I., the order of arrangement of the representation of different parts of the body. We cannot well separate the consideration of this arrangement from that of the order in which the different characters of the movements are placed, hence we will reserve to p. 79 the discussion of the facts set out in Table I.

We will, however, proceed to discuss certain points of general interest upon which a clear opinion must be formed before the main results of this research can be given at length. Of such points we take first, as the most important, the phenomenon of bilateral movement.

Movements of Muscles of the same side as that stimulated.

The phenomenon of bilateral movement occurring upon excitation of one hemisphere has often been approached from its theoretical, experimental, and clinical aspects. It has been assumed by Broadbent* that this is effected by the impulses passing from the sound hemisphere across commissural fibres postulated to exist between the lower (*i.e.*, bulbo-spinal) centres of the two sides, and he explained the common mode of recovery from hæmorrhagic compression and destruction of the internal capsule by this theory. This theory has been favourably received by neurologists as an explanation of the phenomenon of bilateral movement, but we submit that the subject can only profitably be treated upon experimental facts as a basis.

Before any satisfactory conclusions can be arrived at, we must obviously first determine exactly how much bilateral representation of movement exists in the cortex of a normal uninjured nervous system, and, in this case, of the Bonnet Monkey. Further we must understand clearly what we mean by bilateral representation.

Beginning with this last, we mean that the same movement of symmetrical parts of both sides of the body is represented in one point of the cortex of both hemispheres, *i.e.*, that excitation of such a point evokes simultaneous and identical movement in the same part of both sides of the body.

In attempting to classify "bilateral movements" it is necessary to point out first that movements such as conjugate deviation of the eyes are not, strictly speaking, examples of bilateral representation. For while it is true both eyeballs move, nevertheless one is rotated out, the other rotated in, and since this conjugate deviation occurs as the result of a single idea, the movement of both eyeballs really corresponds to that of one limb, and this is more especially the case since, as just said, the muscles employed on each side are different. A final confirmation of this view lies in the fact that excitation of one hemisphere produces conjugate deviation in one direction only, while excitation of the other evokes an exactly opposite movement.

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* 'British Medical Journal,' vol. 1, 1876, pp. 333, 371, 401.

To this point we shall subsequently return. We may now mention the movements which are credited with being bilaterally represented, and we shall arrange them in classes, the justification for which will subsequently appear.

Credited as Bilateral.

Movements of Trunk Muscles (*i.e.*, Rectus, abdominis, &c.)		Class I. Not bilateral, *vid. inf.*
Movements of Tongue		
Conjugate deviation of Eyes		
Turning of Head		
Retraction of Angle of Mouth		Class II. Imperfectly bilateral.
Pursing of Lips		
Opening of Eyelids	Identical movement	
Closing of Eyelids		
Pouting of Lips		Class III. Truly bilateral.
Mastication		
Swallowing (*i.e.*, movements of soft palate)		
Adduction of vocal cords		

Class—I. *Movements asserted to be bilateral, but not actually so.*

Movements of the Trunk Muscles.—The muscles of the trunk have above all others in the body been commonly supposed to be bilaterally associated in action. This is, however, quite contrary to observed fact. We have never seen any movement of both recti or oblique abdominis follow excitation of the fibres for the trunk muscles in the capsule, although we invariably saw movement restricted to the muscles of the opposite side, notably the rectus. We have observed this to be the case clinically, and believe that the statements made in the opposite direction rest upon imperfect examination. Further confirmation is to hand in the description given by Professor SCHÄFER* and one of us, of the results of excitation and ablation respectively of the "trunk areas" in the marginal gyrus, from which it appears that the same unilateral representation was discovered to exist.

Movements of the Tongue.—As we are specially investigating the cortical representation of these movements, we desire to defer the detailed observation of the capsular fibres subserving the same, until the former is completed.

Conjugate Deviation of the Eyes and Turning of the Head.—We have already mentioned the movements of the eyeballs, and we now intend to strengthen what is said on p. 73.

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* HORSLEY and SCHÄFER, 'Phil. Trans.,' B, vol. 179, 1888, pp. 10 and 14.

We there showed that the deviation of the eyes was a combined movement of opposed muscles (*internal* rectus with *external* rectus) of both sides of the body to produce one effect, and that the opposite hemisphere, when excited, produced exactly the opposite effect.

Further, considering that the visual field is hemiopic, and that the two eyes always have their axes parallel (when not accommodated for near objects), we may look upon the two eyes as acting like one, and we may also regard their movements to be of the same kind as those of the head.

Stimulation of the left cortex produces movement of the head and also of the eyes to the right, and, conversely, when the right cortex is irritated these parts move to the left. Movement to the same side is never observed, hence these movements we regard as distinctly unilateral.

Class II.—Imperfectly Bilateral Movements.

(a.) *Opening of Eyelids.*—In 'Phil. Trans.,' B., 1888, p. 241, we describe how we observed in one Monkey that there were two millimetre-squares on the cortex, excitation of which caused opening of the opposite eyelids to occur before those of the same side. In the present research we have obtained the same result from the internal capsule in one case (Monkey No. 69), at points 50–55 (whole capsule, 100), the movement being also stronger.

The extreme rarity of this phenomenon—occurring, as it does, only twice in about seventy different experiments in the same variety of Macacus—makes it clear that the movement of *opening* the eyelids is practically bilaterally represented. However, the phenomenon is not without interest in discussing the evolution of function in the "motor" cortex.

(b.) *Closure of Eyelids.*—In contradistinction to what we find with regard to opening of one eye before the other, we have obtained closure of the opposite eyelids, not only taking place before those of the same side, but even independently of the eyelids of the same side.

We drew attention for the first time to this differentiation of cortical representation of the eyelids in our second paper just referred to, where we described the opening of one eye before the other. Since writing that paper, we have been engaged in investigating the cortical representation of closure of the eyes, and we have found that there is a nearly horizontal zonular strip of the cortex just below and slightly overlapping the lower border of the upper limb area of representation, in which the single movement of closure of the opposite eyelids is represented.

In some cases this is imperfect, *i.e.*, the eyelids of the side stimulated closed as well as those of the opposite side. It is clear, therefore, that this movement is only imperfectly bilateral, a fact of the greatest importance, as is evidenced by the fact that we have been able with this observation to correctly diagnose that the homologous portion of the cortex in man was the seat of an irritative lesion.

Hence we were not surprised to find that in the internal capsule there were fibres, excitation of which produced closure of the opposite eyelids only.

(c.) *Pursing of the Lips.*—This is another imperfectly bilateral movement, it being most marked always on the opposite side.

(d.) *Retraction of the Angle of the Mouth.*—Rarely have we observed truly bilateral, *i.e.*, symmetrical, retraction of the angle of the mouth, this being the exception to the rule of retraction to the opposite side.

Class III.

(a.) *Pouting of the Lips.*—This eversion of the lips appears to be truly a bilateral movement.

(b.) *Mastication.*—So far as we have been able to observe, this complex movement is mainly bilateral, but we are compelled to postpone its detailed consideration until our analysis of its cortical representation is complete.

(c.) *Swallowing, including movements of the Soft Palate.*—This in our experience of the capsule has always been bilateral on excitation.

(d.) *Adduction of the Vocal Cords* has been shown [*] to be perfectly bilaterally represented.

(e.) *Bilateral Movement of both Elbows.*—This (as flexion) we have found to occur four times altogether in our experiments, when the internal capsule of one side has been excited. The occasions, however, on which this was observed were so few, and the movement so slight and limited that we cannot regard it to be a proof of bilateral representation of this segment of the upper limb in one hemisphere. Moreover, during a long series of experiments upon the cortex this was never observed.

The explanation of this phenomenon we prefer to postpone until further knowledge makes its discussion profitable.

It occurred at point 57, and only in the central [†] Groups, Nos. IV., V., VI.

To sum up, therefore, we consider the following movements to be alone truly bilaterally represented.

Pouting of Lips.
Mastication.
Swallowing.
Adduction of the Vocal Cords.

It will now be expedient to describe the general results obtained by the various groups of experiments.

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[*] KRAUSE, in the Dog; SEMON and HORSLEY, in the Monkey. This is denied by MASINI, and by GAREL and DOR.

[†] *I.e.*, opposite the middle level of the capsule.

Lateral Arrangement of the Excitable Fibres in the Internal Capsule.

We now introduce a new branch of this subject, namely, the relations in lateral juxtaposition of the efferent fibres.

So far we have described the antero-posterior arrangement of these fibres, but we have postponed the consideration of the results obtained by exciting the capsule in individual points of its breadth.

As the capsule varied in width from 1 to 3 mm., and as the part of the sections involving the inner zones of the lenticular nucleus was also constituted of white fibres in and around those zones, we have sometimes found five rows of excitable points (each 1 mm. square). The result obtained from these points we shall now analyse. Altogether we were able to obtain two or more rows of 1 mm. squares in 26 experiments.

Anatomically speaking, in horizontal transverse section we may regard the fibres of the internal capsule as falling into three groups, viz. :—(*a*) those in the mid line ; (*b*) those next the lenticular nucleus, and (*c*) those on the inner side next the optic thalamus, &c.

Of the 26 cases above-mentioned, in seven the excitability appeared to be equally distributed throughout the breadth of the capsule. However, besides these seven, we found that in 15 the most excitable part was that next the lenticular nucleus, this gradually decreasing towards the optic thalamus, but in the remaining four the capsule was most excitable alongside of the thalamus. Considering the anatomical arrangement of the cortex mantle to the position of the basal ganglia and internal capsule, it is not at all improbable that these results may be referable to the fibres entering the capsule from above in an oblique direction, and hence in a horizontal section, they will offer for excitation not only a transversely cut end alongside the lenticular nucleus, but also longitudinal surfaces, which are progressively less and less exposed to excitation as we move across the capsule from the lenticular nucleus to the optic thalamus.

If correct, this view would postulate the theory that the fibres forming the part of the capsule nearest the middle line are inexcitable. This, at any rate, is evidently strongly suggested by the experiments. Moreover, in a frontal microscopic section of the region, the fibres which emerge from the gyrus fornicatus on reaching the capsule, are seen to occupy the most internal position therein, and excitation of the gyrus fornicatus has always failed to elicit movement.

To sum up this question, it is self-evident that, the lateral arrangement of the fibres is infinitely less important than that of the antero-posterior direction, and principally because the function of each point in any given transverse row of squares is the same in character though diminishing in intensity, as we pass from the outer to the inner side of the capsule.

TABLE IV.

Groups.																		
I.	Tongue	Mouth opens	Eyes turn	Eyes open	Head and Eyes turn	Head turns	Angle of Mouth	Shoulder	Fingers	Elbow	Wrist	Trunk	Thumb	Hip	Knee	Small toes	Hallux	Ankle
II.	Eyes turn	Eyes open	Mouth opens	Head turns	Tongue	Wrist	Angle of Mouth	Trunk	Shoulder	Fingers	Elbow	Hip	Thumb	Knee	Small toes	Head and Eyes turn	Ankle	Hallux
III.	Eyes open	Eyes turn	Head and Eyes turn	Head turns	Mouth opens	Tongue	Angle of Mouth	Elbow	Shoulder	Thumb	Fingers	Wrist	Hip	Trunk	Knee	Ankle	Hallux	Small toes
IV.	Eyes turn	Eyes open	Mouth opens	Head turns	Head and Eyes turn	Shoulder	Angle of Mouth	Wrist	Fingers	Elbow	Tongue	Thumb	Ankle	Trunk	Hip	Knee	Hallux	Small toes
V.	Eyes open	Mouth opens	Eyes turn	Head turns	Head and Eyes turn	Tongue	Angle of Mouth	Elbow	Shoulder	Fingers	Trunk	Thumb	Wrist	Hip	Knee	Hallux	Small toes	Ankle
VI.	Eyes turn	Eyes open	Tongue	Head turns	Mouth opens	Elbow	Shoulder	Angle of Mouth	Thumb	Wrist	Fingers	Hip	Ankle	Knee	Trunk	Hallux	Small toes	
VII.	Eyes turn	Eyes open	Head and Eyes turn	Head turns	Tongue	Trunk	Angle of Mouth	Shoulder	Wrist	Elbow	Thumb	Fingers	Hip	Ankle	Hallux	Knee	Small toes	
VIII.	Eyes turn	Eyes open	Angle of Mouth	Elbow	Shoulder	Head turns	Fingers	Trunk	Wrist	Small toes	Hallux	Ankle	Thumb					

Character of the Movements of the Parts Represented in the Fibres of the Internal Capsule.

We have given at pp. 60–63 the antero-posterior arrangement in the capsule of the movements of the different parts of the body (see Table), we now furnish two tables (see Tables IV. and V.) in the latter of which again taking the whole capsule as 100, the extent of representation of each kind of movement of the several parts of the body is given.

We wish first to review the Table IV., given on p. 78, in detail, to see how far the order of arrangement of representation of parts, *i.e.*, independently of the character of the movement of such parts in the capsule, agrees or disagrees with the arrangement which we have shown to exist in the cortex.

The accompanying diagram (fig. 7) the details of which we have partly published in the 'Philosophical Transactions,' 1887–88, the remainder being in course of publication, gives in bare outline the relative positions of the points of chiefest representation as we have found them, by minimal excitation, to exist in the cortex of the Bonnet Monkey (*Macacus sinicus*).

With this outline before us we would suggest that the main axes of the fibres of the internal capsule correspond as far as antero-posterior arrangement goes with lines drawn at right angles to the direction of the upper two-thirds of the fissure of ROLANDO. It also remains to be seen whether there is any relation between the arrangement in the cortex in the horizontal antero-posterior division and the order of fibres in the capsule.

Table IV. contains the antero-posterior arrangement of the average position of the representation in the capsule of the various parts of the body, set out horizontally. Although each observation is placed vertically under each other, this is not necessarily true of their anatomical position, as we have already shown.

It substantiates our view that the oblique lines over the "motor" cortex described above give truly the order of representation in the capsule. For while the movements of opening the eyelids and of the eyes are seen to occur in front in both cortex and capsule, those of the toes are equally the most posterior. Hence placed in order from before back we have eye movements, head movements, upper limb movements, trunk and lower limb movements.

Or stating in further detail the order of the representation as given in the foregoing table in the average position of each segment in each part of the body, the following general order of representation is arrived at, viz. :—

Summary of averages :—

44	Eyes open	Eye movements
42	Eyes turn	
50	Mouth opens	
50	Head and eyes turn	Head movements
52	Head turns	
53	Tongue	
60	Angle of mouth	
62	Shoulder	Upper limb movements
64	Elbow	
66	Wrist	
66	Fingers	
70	Thumb	
70	Trunk	
76	Hip	Lower limb movements
77	Ankle	
78	Knee	
78	Hallux	
80	Toes	

Further, if we state for each of these their relative positions to the whole of the capsule, we obtain figures which give the relative positions absolutely as above shown by the numbers placed at the left hand side of the column.

We draw attention by brackets to the association of parts in movement as already shown to occur in the cortex.

Nothing, we believe, shows more distinctly the truth of our position that the arrangement in the capsule is but an imitation of that on the cortex, which in its turn is but a peripheric projection of the order of the metameres of the whole body.

The accuracy of this general view is borne out by an analysis of the representation of the segments of one, the lower limb. In both the cortex and capsule the hip is most represented in front, the small toes hindermost (*i.e.*, posterior to the hallux), and the other joints intermediately. Similarly, in accordance with the view of SCHÄFER and HORSLEY* that the trunk muscles are represented mediately in the "motor" region, we find that in the capsule the representation of this part is, as a rule, between the upper limb and lower limb regions.

For the upper limb the arrangement in the capsule is analogous to that for the lower limb, namely, the largest joint, the shoulder, is most anterior, and the smallest, the most specialised, the thumb, is most posterior. By dropping verticals in fig. 7, on p. 81, this is evidently the cortical arrangement projected below.

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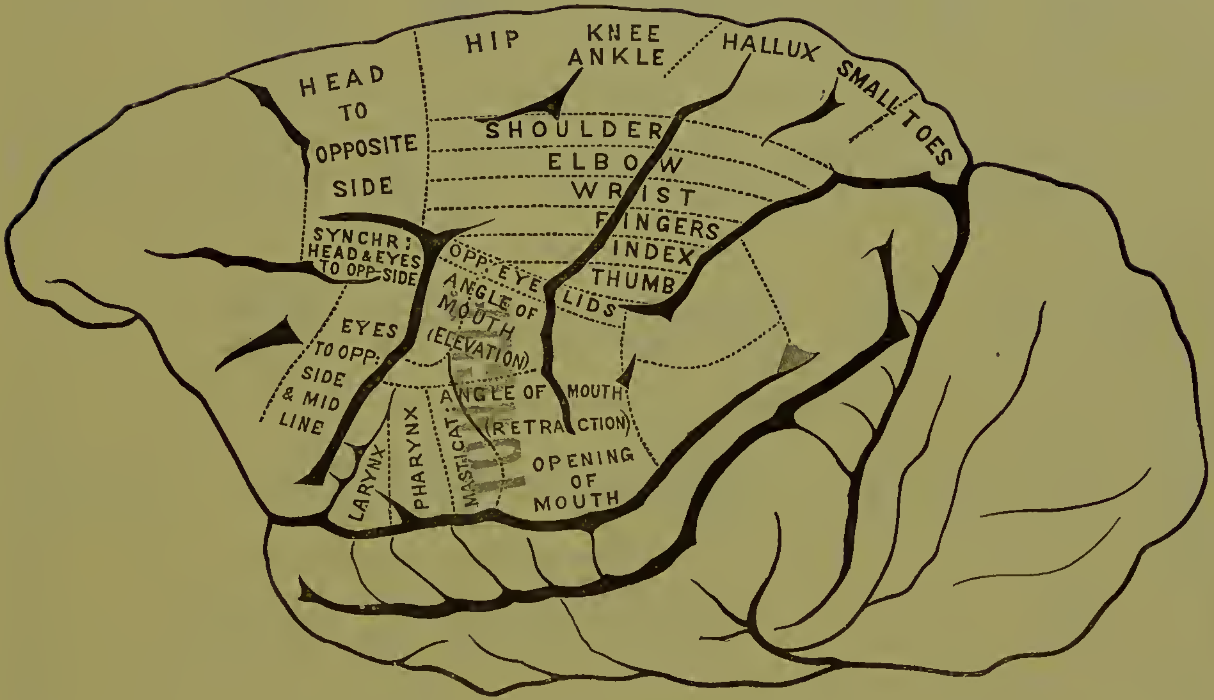
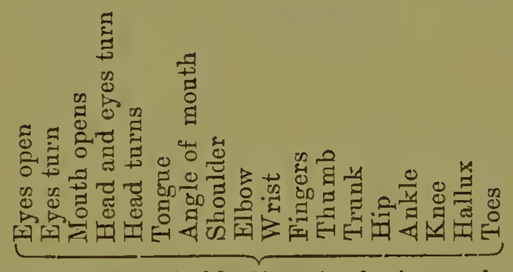
* 'Phil. Trans.,' B, 1888, p. 9; 'Roy. Soc. Proc.,' vol. 36, 1884, p. 437.

Fig. 7.





Arrangement of excitable fibres in the internal capsule.

Drawn from a photograph (magnified twice) of the outer surface of a Monkey's (*Macacus sinicus*) left hemisphere.

TABLE V.—(Length of Capsule = 100.)

Kind of Movement.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
Eyelids, both sides open	24–25	37–61	41–62	30–60	38–54	40–64	5–51	16–41
,, opposite side more than same side	..	..	..	..	50–55			
,, both sides close	..	..	..	66–75	100 (1 observ.)	..	33	
,, opposite side alone closes	..	..	67–77	..	60-65	64	60–62	75 (1 observ.)
Eyeballs become parallel	..	..	..	49–51	40	..	33	
,, turn to opposite side	22–60	25–68	48–60	23–57	38–59	42–60	5–51	8–41
,, turn to opposite side and downwards	8–16	..	..	..	25–60			
,, turn up and to opposite side	..	..	..	..	..	..	5	
Pupils dilate	..	..	..	42	45	..	..	16–25
Head and eyes turn synchronously to opposite side	41–54	..	53–60	55	53–60	..	29–35	
Head turns to opposite side	42–64	42–71	56–70	34–65	41–58	47–66	22–45	33–66
,, turns, muzzle up	52							
,, retracted	..	..	75	65–90 (1 observ.)				
Lips, depression of opposite lower	..	..	..	..	54–68			
,, pouting of both	..	56	..	..	..	..	..	41–50
,, pursing of both, but especially on opposite side	..	..	..	65	..	63		
Angle of mouth,* opposite retracted	58–82	48–83	58–79	50–85	54–80	51–78	45–65	16–50
,, both sides retracted	..	..	58	..	..	63		
Mouth opens	13–51	43–57	57–71	40–62	44–48			
,, shuts	..	25–37	73 (1 observ.)					
,, opens and shuts (as in mastication)	14–69	44–47	77	45–47	61–63	88–94 (1 observ.)	45	
Tongue protruded straight	7–24	57–61	47	52–69	64–65	55		
,, ,, to opposite side	..	..	..	66–83	57–62	..	35–47	
,, ,, to same side								
,, ,, to same side (concave to opposite side)	..	..	73					
,, narrowed	..	..	78	..	75–80			
,, retracted, heaped up posteriorly	..	..	52	63	76			

* We have not in this paper differentiated between elevation and retraction of the angles of the mouth.

TABLE V.—continued.

Kind of Movement.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
Tongue retracted, tip retracted	..	..	..	77	64–69	..	52	
,, ,, and protruded	..	50						
(1) to same side	..	50						
(2) to opposite side	..	..	77					
,, heaped behind, rolled, and protruded to same side	..	..	68	61–72	65–72			
Swallowing	..	..	..	65				
Barking	..	..	36					
Shoulder, advancing	62–76	..	74–82	62–63	66–79			
,, retract	..	..	75	80	59	55		
,, adduction	..	68–86	75–83	60–83	66–80	65–89	45–62	49–66
,, abduction	..	..	77	40	..	..	..	16–25
,, rotation in	..	56	..	77	65	..	66	41–58
,, rotation out	67–70	63–70	67	59	55–71	..	51–54	16–50
Elbow, extension	70	58–62	66–73	60	57–59	55–61	41	17
,, confusion	75–91	68–74	75–80	58	70–76	57–67		
,, flexion	60–91	69–86	70–87	57–83	66–79	57–77	51–65	33–62
Wrist, extension	75–100	63–73	75–90	58–74	65–76	68–72		
,, flexion	..	..	64–73	60	78	..	62	
,, pronation	80	..	89–100	45–72	67–71	65–69	70	62
,, supination	..	..	..	55–63	68	..	41–64	41–50
,, ulnar adduction	..	..	..	..	..	69	..	50
,, confusion	..	..	..	..	..	60		
Index finger, flexion	..	..	..	..	..	60–69		
,, flexion, extension	..	..	..	..	..	65		
Fingers, extension	..	61–72	65	62–68	67–71	57–61	50	
,, extension, flexion	66	..	83					
,, interosseal flexion	91–100 (1 observ.)	..	84–90	..	50			
,, flexion	65–77	65–86	75–82	62–79	63–85	68–82	62	37–62
,, confusion	..	77						
Thumb, extension	..	61	..	70 (1 observ.)	79	65	55	
,, extend, flexion	..	..	94 (1 observ.)					

TABLE V.—continued.

Kind of Movement.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.
Thumb, interosseal flexion	83–87	..	82–88	..	76			
,, flexion	71–76	79–88	78–87	65–81	68–80	62–73	61	62
,, flexion, extension	..	..	..	..	..	65		
,, abduction	..	..	..	45–50				
Trunk, opisthotonus	70–76							
,, rotation to opposite side	..	61–72						
,, arching to opposite side	..	..	60					
Abdomen, opposite rectus	70–88	60–80	80–86	80	58–85	77–83	41–58	
Tail, adduction or flexion to opposite side	..	..	87					
,, extension to opposite side	..	..	84	..	..	77–88		
Hip, extension	100	83	88	..	52–71			
,, confusion	..	77	81–87					
,, flexion	62–71	85–90	74–85	74–91	72–76	68–79	65	
,, adduction	..	75	88	..	85–90			
,, rotation out	85–89	..	..	85–90	68–70			
,, rotation in	..	68–81	..	83	75–85	69		
Knee, extension	100	..	78–82	..	75			
,, confusion	..	77	84					
,, flexion	79–83	81–93	84–86	76–88	74–77	76–82	66	
,, rotation in	..	..	78					
Ankle, dorso flexion	78–81	92–96	83–89	73–82	83–88	72–85	64	58–78
,, plantar extension	100	83	88–90	66	73	83	..	41
,, eversion	88–94	..	77–94	..	78–82	69		
,, inversion	..	87–93	78	85–90	71	77		
Small Toes, extension	91–95	84–94	86–92	76–94	82–86	82–88	61–72	58–66
,, interosseal flexion	..	..	88–100					
,, flexion	71	83	86	72–80	82	69	..	41–66
,, flexion, extension	70–76							
Hallux, extension	82–88	92–98	84–91	79–92	72–83	82–88	..	66
,, flexion	73	..	86–95	72–86	78–86	69	..	41–66
,, flexion, extension	70–76							

We are now in a position to point out the chief facts of interest to be noted in Table V., and which illustrate the relation between the localisation of motor or efferent function in the cortex and that in the capsule. Under the drawing, fig. 7, we have inscribed in their accurate relative positions the arrangement of the capsular fibres. If lines be laid obliquely as stated on p. 79, the exact correspondence of the cortical capsular representation will be readily seen.

Movements of Eyelids.

The most striking among these is that of closure of the opposite eyelids only (or in an incompletely evolved cortex accompanied by slight movement of the same side). The cortical localisation of this movement we give in fig. 7, and a line drawn vertically shows it to be relatively far behind the area for the other movements of the lids.

So in the capsule it is found fully one-tenth to one-fifth of the length of the capsule further back, and thus comes into relation with the representation of the upper limb and angle of the mouth. No closer correspondence between the representation in the cortex and that in the capsule could well be imagined.

In passing on to the next feature of special interest we would mention that we only observed the minuter changes in the movements of the lips, mouth, tongue, and jaws towards the end of this work, since our analysis of the facial region (not yet published) has only been carried on during the last fifteen months. Hence our account of these movements is necessarily brief.

Upper Limb Movements.

Elbow.—In describing[*] the analysis of the upper limb cortical representation we have shown that extension of the elbow is represented most anteriorly and superiorly, and flexion most inferiorly and posteriorly, while confusion of these movements is localised between their foci of most intense representation. This is most clearly found to be also the case in the capsule. The elbow, being a simple hinge joint and allowing only of extension, flexion and confusion, affords a ready means for this comparison between the cortex and capsule, and therefore it is interesting to note that in every group of sections this close similarity of representation was established.

Fingers.—So also the hinge joints of the fingers show that extension is represented anteriorly and flexion posteriorly in the capsule, this difference being, as seen in Table V., present in every group.

Thumb.—The same also prevails for the thumb.

Lower Limb Movements.

Since the cortical representation of the movements of the lower limb was shown by our analysis to be relatively imperfect, it was to be expected that with the mingling of fibres in the capsules, still less differentiation would be found. This is obviously shown in Table V., but on inspection, the representation of even flexion of the *small toes* is consistently (every group) in front of that of extension. To a minor degree and with less consistency (4 of 6 groups) the same holds for the hallux.

---

[*] 'Phil. Trans.,' B., 1887-88.

Relative Amount or Degree of Representation of Extension compared to Flexion.

This subject may not be without interest to those who have, from excitation experiments, attempted to gauge the relative amount of functional activity in the cortex.

The facts bearing upon this point obtained from the records of hinge joint movements are so clear and unmistakable that they are of value.

The following are the proportional rates of frequency as observed in the capsule.

	Flexion.	Extension.	Remarks.
Elbow	38	16	Joints whose usual movement is powerful flexion
Fingers . . .	38	17	
Thumb . . .	22	9	Joint the flexion of which is usually carefully regulated by extension
Small toes . .	15	26	Joints very frequently spread in extension for standing
Hallux . . .	16	17	Joint used as a thumb as well as for support

The bearing of these facts obviously requires no further comment, and the more so as they are but confirmatory of the results we obtained in our analysis of the cortical representation of these parts.

CONCLUSIONS.

As the foregoing paper is but a collection of detailed facts we can only offer as conclusions a few bare statements.

1. The fibres of the excitable portion of the internal capsule are arranged from before back, in the same order as the foci of representation in the excitable part of the cortex, taken along lines drawn at right angles to the direction of the fissure of ROLANDO.

2. This applies to the great divisions of the body, *i.e.*, head, upper limb, &c.

3. The arrangement of the fibres for the different segments of each great division is likewise that which prevails in the cortex.

4. Similarly the character of each movement is represented in the capsule as in the cortex.

Description of Plates.

PLATES 5.–9.

Fig. 1. This figure consists of a number of drawings of the internal capsule and basal ganglia of the left side in horizontal section, corresponding to the eight different levels into which we have grouped our observations, and enlarged twice the natural size.

a. = Anterior commissure.
C. = Caudate nucleus.
F. = The point of fusion of the lenticular and caudate nuclei in the basal grey matter.
i. = Inner zone of the lenticular nucleus.
l. = Middle zone of lenticular nucleus.
L. = Outer zone of lenticular nucleus or putamen.
O. = Optic thalamus.

Figs. 1, A.–R., give on tracings of the outlines of fig. 1, the limitation of the fibres, excitation of which produced a particular movement, the character of which is indicated in the margin.

Figs. 4, 5, 6 (on Plate 6). Views of a dissection of the hardened brain of a *Macacus sinicus,* in which almost the whole of the hemisphere has been cut away, leaving only the basal ganglia to show their relations to each other and to the internal capsule. Fig. 4 is viewed from the inner or ventricular side, fig. 5 from below, and fig. 6 from the outer side.

A.a. = Anterior and ascending division of præfrontal fibres, lying in the deep groove between the caudate and lenticular nuclei.
a.c. = Anterior commissure.
Ch. = Optic chiasma.
Cb. = Cerebellum.
H. = Horizontal fibres of præfrontal portion of capsule.
Hi. = Hippocampus major.
Gy.Hi. = Gyrus hippocampi.
C.q. = Corpus quadrigeminum.
l.m. = Outermost lamina medullaris.
s.d. = Superior and descending division of præfrontal fibres.
Ca. = Caudate nucleus.
Pu. = Putamen or outer zone of lenticular nucleus.
P.F. = Excitable ("motor") or fronto-parietal fibres.
L. = Posterior limit of excitable fibres.

Note change of direction at this point opposite middle zone (m) of lenticular nucleus, the fibres forming the internal capsule behind and below (m) are respectively occipital, occipito-temporal, and temporal.

M.C. = Middle commissure.

III., V., and VI. denote the third, fifth, and sixth cranial nerves.

PLATE 10.

Groups I.–VI. These are photographs typical of each level at which we have excited the capsule, corresponding to the first six groups of our observations.

Ca. = Caudate nucleus.
Le. = Lenticular nucleus.
O.Th. = Optic thalamus.

PLATE 11.

Groups VII. and VIII. These are photographs of our last two levels and follow on Plate X.

NOTE.—Group VIII. has been reversed in the reproduction.

The section is taken from the left hemisphere, except in Groups IV. and VIII., which are taken from the right side.

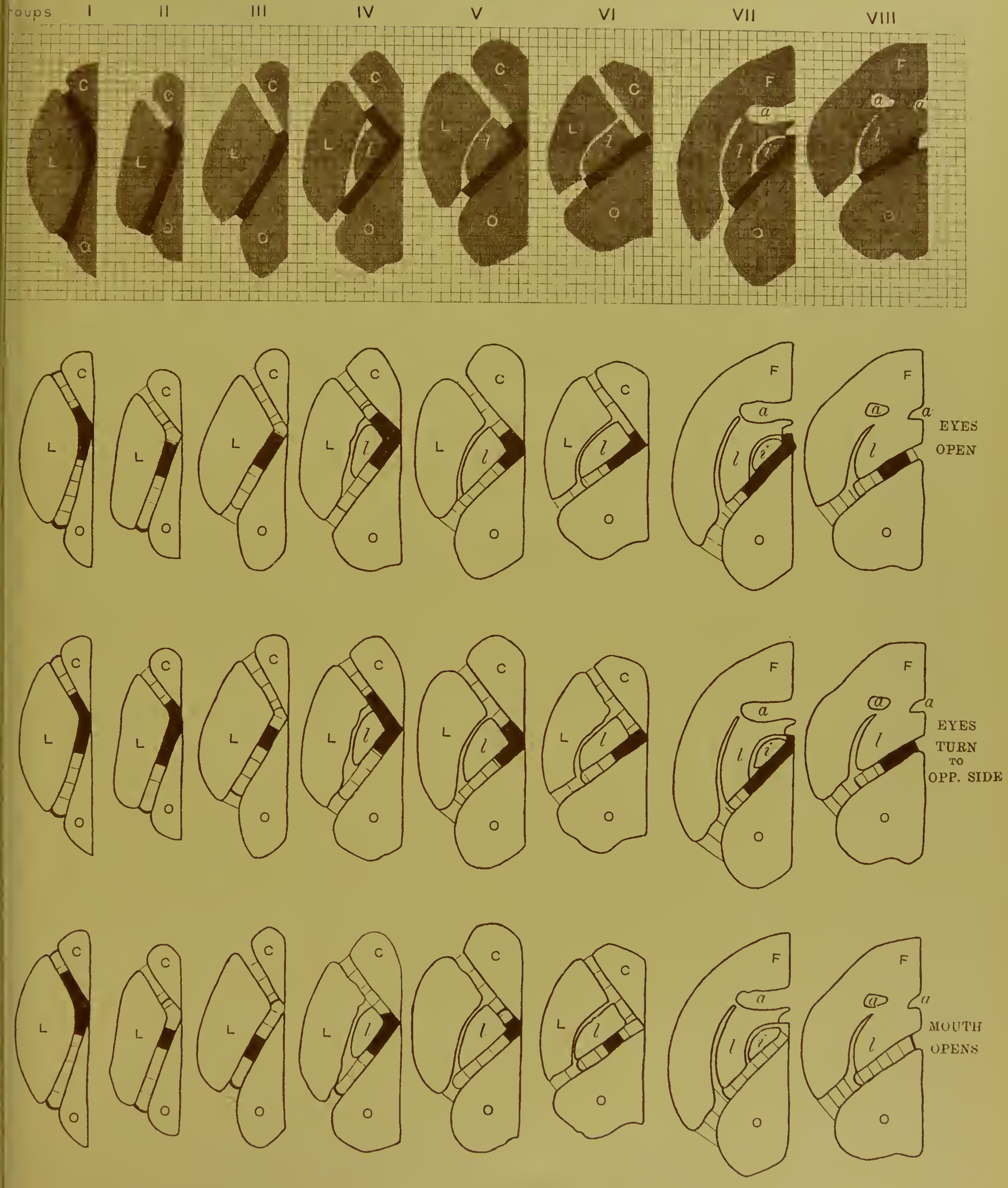
Fig. 2. A photograph of a transverse vertical section of the right hemisphere of *Macacus sinicus*, showing the limits of the capsule and the direction of its anterior limb in frontal section.

Ca. = Caudate nucleus.
C.c. = Corpus callosum.
Le. = Lenticular nucleus.
S.l. = Septum lucidum.

Fig. 3. This figure is a photograph of a sagittal section of the hemisphere of a *Macacus sinicus* stained by PAL's method and mounted in balsam. The medullated fibres are consequently stained black, the grey matter being of a lighter greyish tint.

A.a. = Anterior or ascending fibres of præfrontal division of capsule.
H. = Horizontal fibres of the same.
S.d. = Superior or descending fibres of the same.
P.f. = Pyramidal fibres (excitable).
P. = Fibres entering the posterior limb of the capsule.
Ca. = Caudate nucleus.
Le. = Lenticular nucleus.
O.th. = Optic thalamus.
A.c. = Anterior commissure.

Fig I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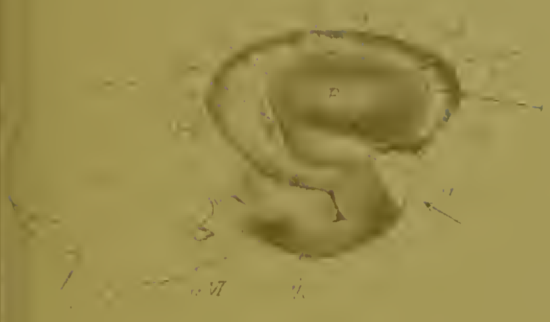


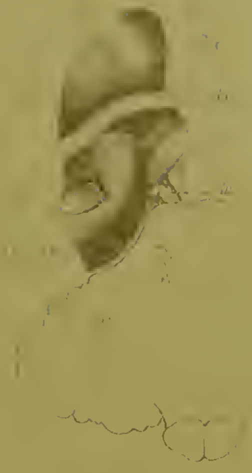


Fig. 5

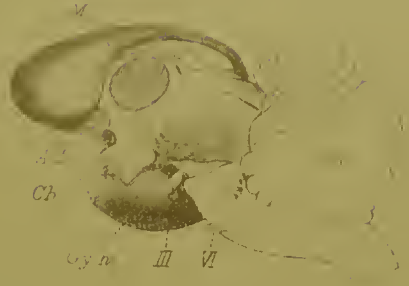
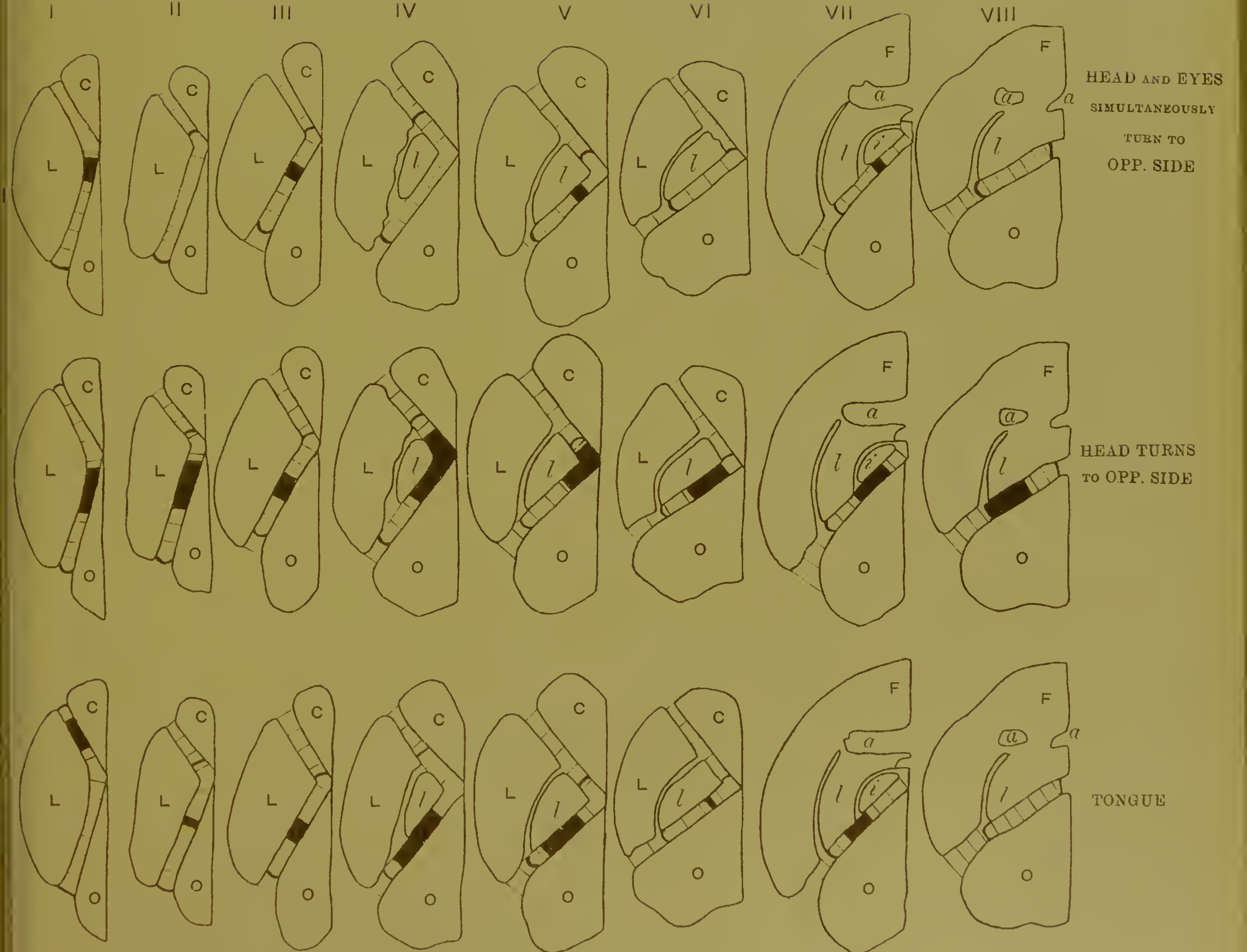


Fig. 4

g I. Contd



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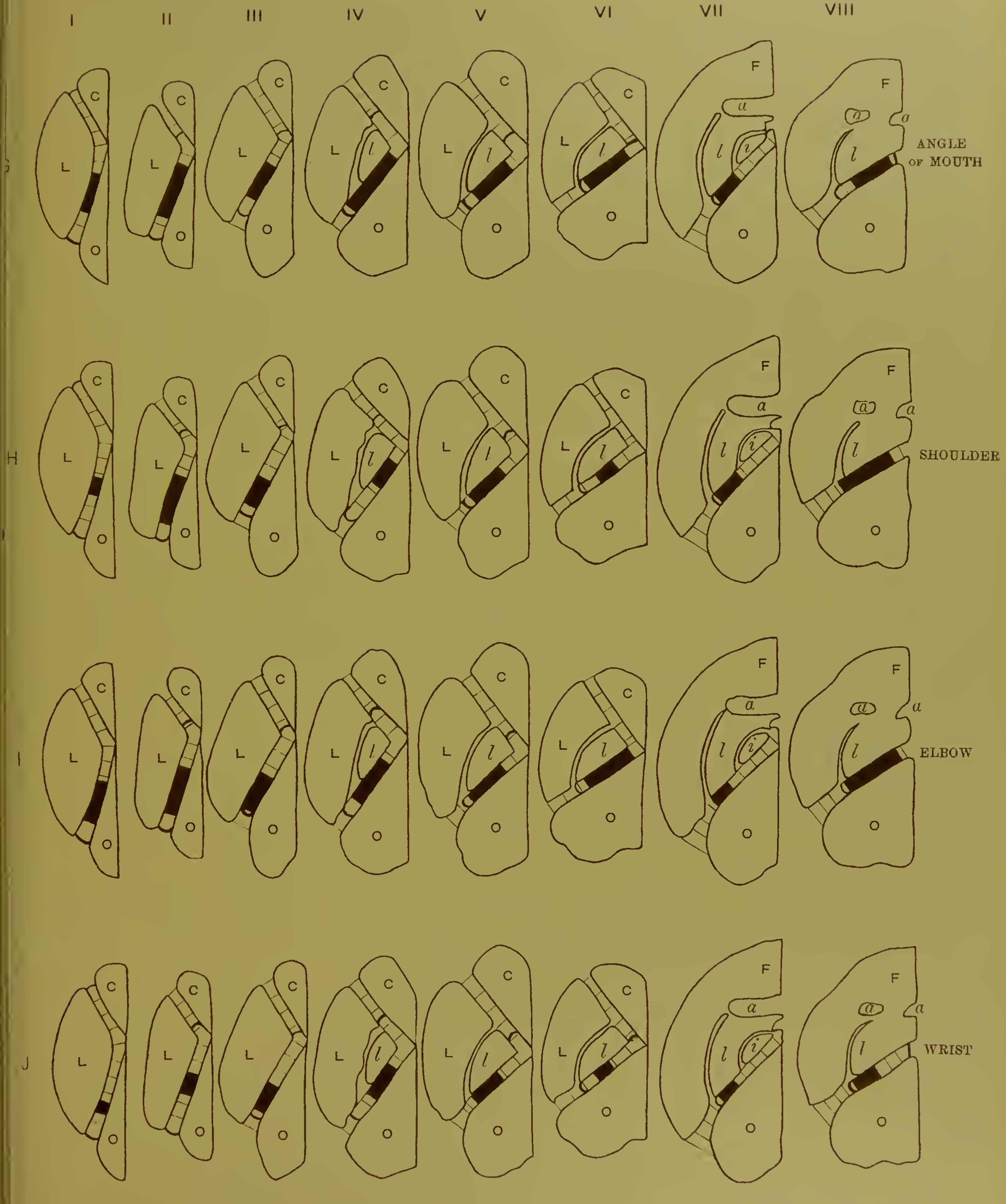
Beevor & Horsley

Phil. Trans. 1890. B. Plate 7



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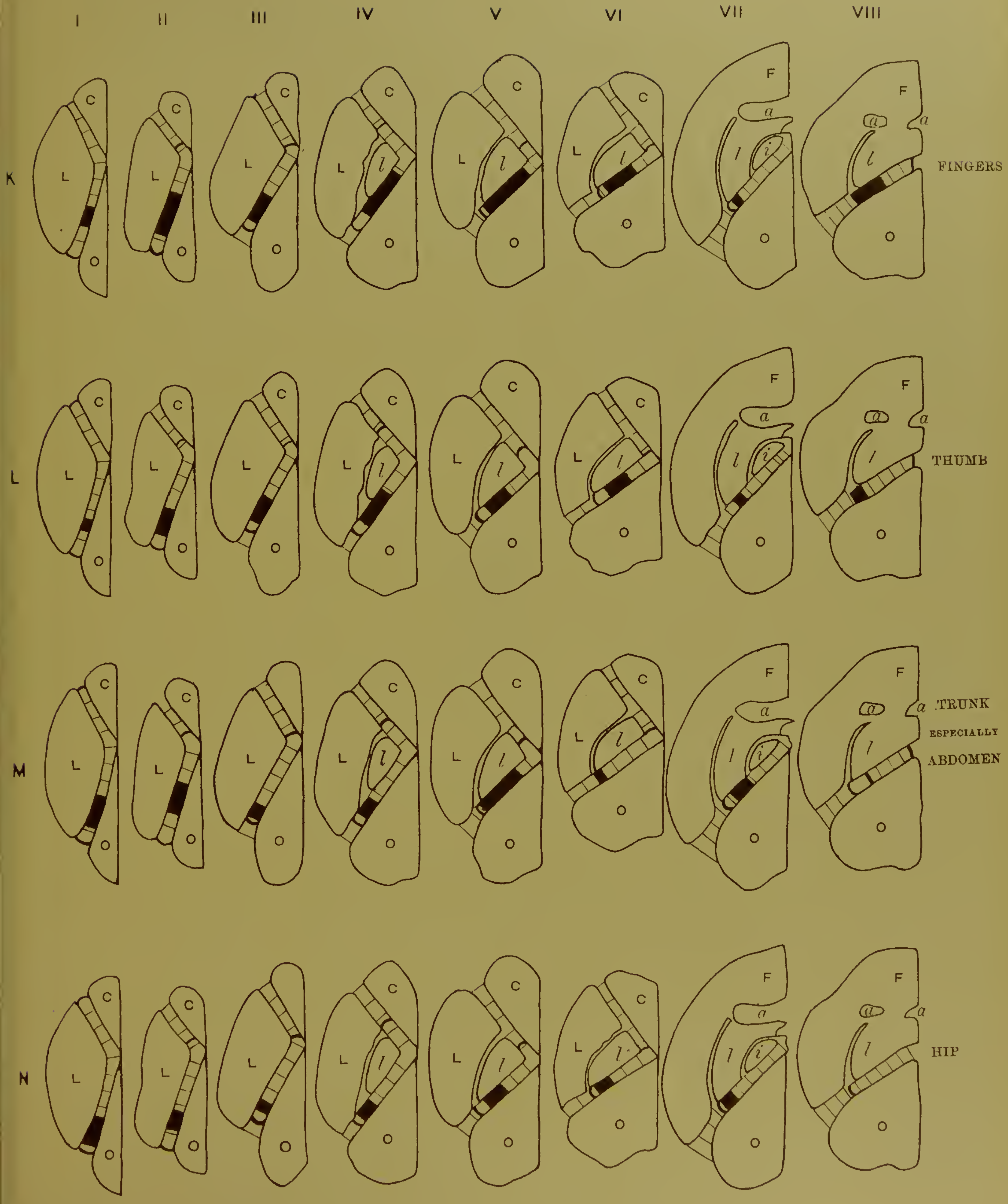
I
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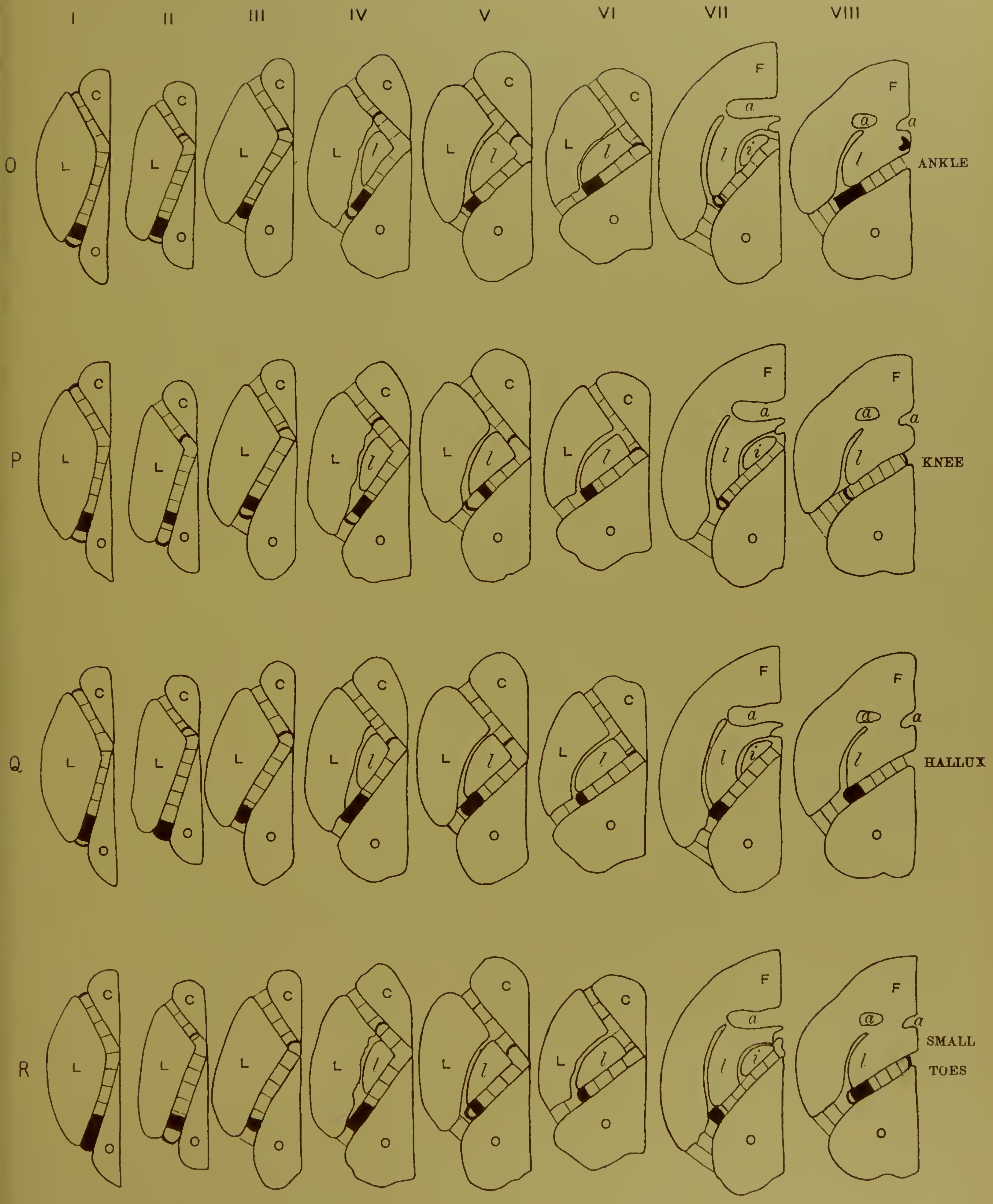
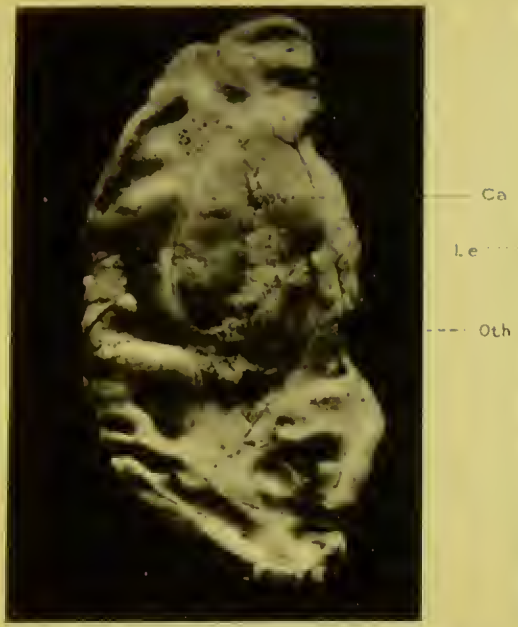
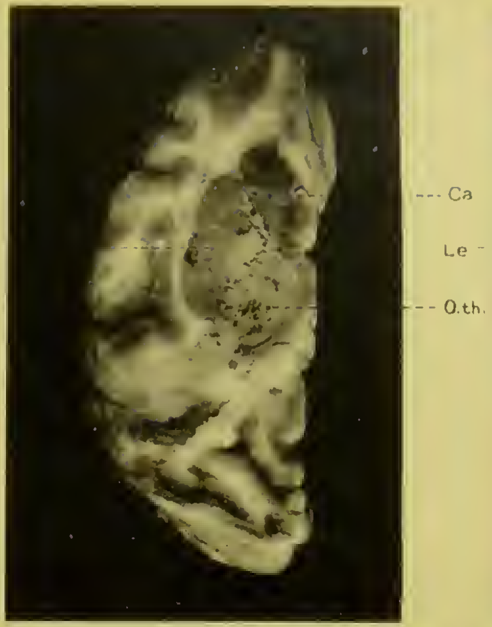


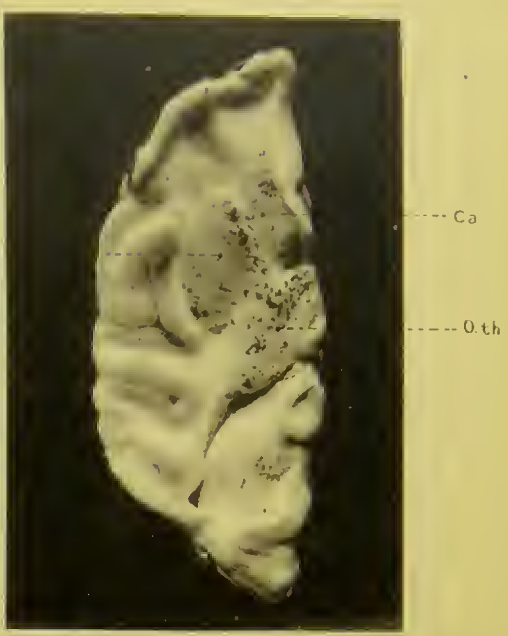
Lith & Imp. Camb. Sci. Inst. Co.



Group I

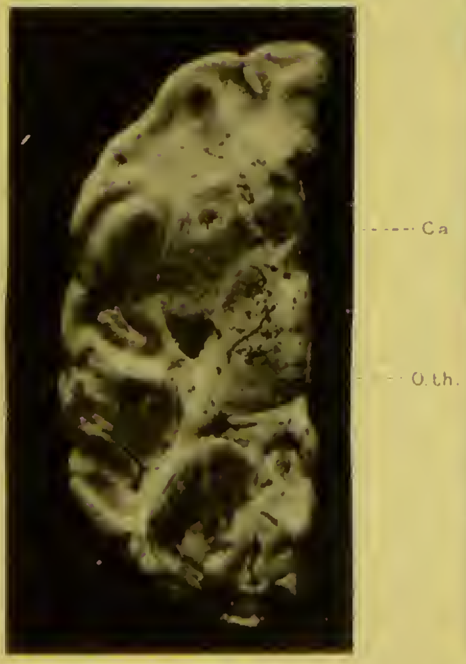


Group II

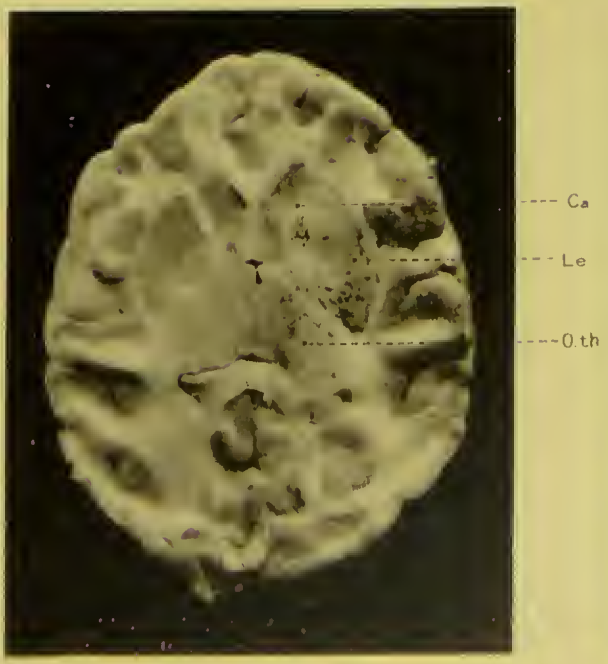


Group III.

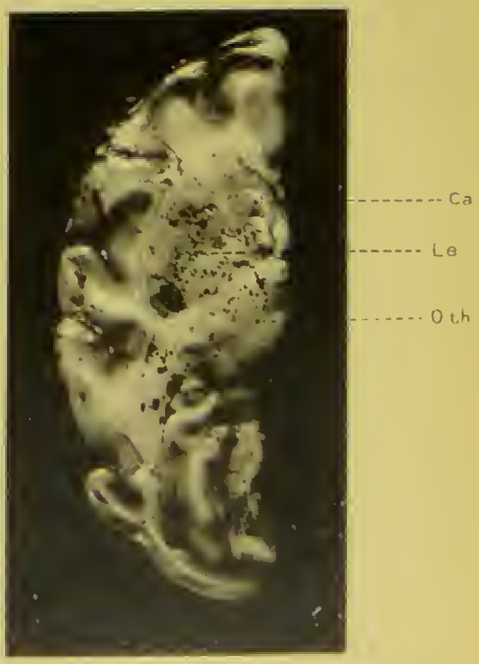
Group V.



Group IV.



Group VI.



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III. *A Further Minute Analysis by Electric Stimulation of the So-called Motor Region (Facial Area) of the Cortex Cerebri in the Monkey* (Macacus sinicus).*

By Charles E. Beevor, *M.D., F.R.C.P., and* Victor Horsley, *M.B., F.R.C.S., F.R.S. From the Laboratory of the Brown Institution and from the Pathological Department of University College, London.*

Received March 22,—Read May 18, 1893.

[Plates 8, 9.]

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Introduction.

In continuation of our former minute analysis of the excitable region of the cerebral cortex, we have explored the so-called centres for the facial, lingual, and pharyngeal movements, or as we prefer to speak of them collectively, the facial area. This district, as will presently be seen, has been mapped out by numerous investigators, and its general limits are fairly well understood; but as we have found in the course of our investigations several points untouched, especially relating to the representation of the movements of the tongue, we think it better to arrange the facts previously determined in an historical introduction and to subjoin our own observations. In this, as in our second paper[*] on the minuter representation of movements in the cerebral cortex, we have, in order to avoid discrepancies in the arrangement of the sulci, employed only the same variety of Monkey, viz., *Macacus sinicus.* In all we have performed twenty experiments.

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* The expenses of this research were defrayed principally by an assignment from the Government Grant administered by the Royal Society, and in part by a grant from the Scientific Grants Committee of the British Medical Association.

HISTORICAL INTRODUCTION.

FRITSCH[†] and HITZIG, in the original memoir which forms the basis of all modern research on the subject, contented themselves with defining the foci of representation of movements of the face in the Carnivora.

HITZIG[‡] later investigated the point in the Monkey. In his paper on equivalent regions of the brain in Dogs, Monkeys, and Men, HITZIG describes an excitation experiment on a Monkey (*Inuus rhesus*). The representation of facial movements he obtained in this case was as follows :—The highest point of the facial "region" was "centre 3" and is figured by him as just above the genu of the fissure of ROLANDO and in the ascending frontal gyrus. At this point he obtained closure of the eye and retraction of the ear. Below this point, excitation elicited, in addition to the ear movement, contraction of the masseters, then movement of the lips, and finally, at a point just above the fissure of SYLVIUS, the current produced opening (*aufsperren*) of the mouth. Just above this latter place he obtained retraction of the angle of the mouth, and in neighbouring parts movements of the tongue muscles, depressors of the jaw, elevators and depressors of the hyoid bone. All these latter-named movements were *bilateral.*

FERRIER.[§]—FERRIER, in the Monkey, determined four points in which are represented movements of the facial muscles and tongue, as follows :—

No. 7. (Situated on the ascending frontal gyrus apparently just opposite and below the genu of the fissure of ROLANDO, see further, "Anatomy," p. 4), "Retraction and Elevation of the Angle of the Mouth and the Action of the Zygomatic Muscles."

No. 8. (Situated just below and above sulcus *v*, see further, "Anatomy," p. 4), "Elevation of the Ala of the Nose and Upper Lip, Associated with Depression of the Lower Lip so as Fully to Expose the Canine Teeth."

No. 9. (Situated on the lower extremity of the ascending frontal gyrus immediately in front of the sulcus *v*, see further, "Anatomy," p. 4), "Opening of the Mouth with Protrusion of the Tongue."

No. 10. (Situated on the lower end of the ascending frontal gyrus between the lower end of the fissure of ROLANDO and *v*, see further, "Anatomy," p. 4), "Opening of the Mouth with Retraction of the Tongue." "These movements" (described under Nos. 9 and 10) "are occasionally repeated for some time after the electrodes are withdrawn. The movements are bilateral."

---

[*] 'Phil. Trans.,' B, 1888.

[†] 'Archiv für Anat. und Phys.' (DU BOIS-REYMOND), 1870, p. 300.

[‡] 'Untersuchungen über das Gehirn,' Berlin, 1874, p. 132.

[§] 'The Functions of the Brain,' 1st ed., 1876, 2nd ed., 1886.

No. 11. (Situated on the lower extremity of the ascending parietal gyrus covering the space between the hinder end of the fissure of ROLANDO and the lower end of the intraparietal sulcus,) "Retraction of the Angle of the Mouth." "The action is that of the platysma myoides, and when this is strong the head is drawn slightly to the side."

H. MUNK* confirmed the fact that the movements of the face and tongue were represented in the Monkey in the area delineated by HITZIG and by FERRIER, but did not record minuter details of the localisation.

SCHÄFER and HORSLEY.†—These investigators found on sub-dividing the facial area, as marked out by FERRIER, that the broad facts described by him were correct, except that the *upper* part of the area was the seat of elevation of the angle of the mouth, and that the *lower* half was the region of retraction of the same. (It may be noted that FERRIER, in the last chapter of his book, when he transfers the excitation results from the Monkey's brain to that of Man, places these areas of representation in the reverse order, *i.e.*, the same as SCHÄFER and HORSLEY, and, as will presently be seen, the same as we have found it, namely, "Elevation" above "Retraction.) They further observed that just below the upper border of the so-called face region, *i.e.*, just opposite to the lower end of the intraparietal sulcus, the movements of winking and of closure (synchronous) of both pairs of eyelids were therein represented; also that half-way down the vertical limit of the præcentral sulcus and just below it, the movement of drawing in and out of both cheeks was elicited on excitation; also that pouting and pursing of the lips were evoked from the horizontal strip of cortex running forwards from the lower end of the fissure of ROLANDO towards the præcentral sulcus; finally, from above the Sylvian fissure and between the lower end of the fissure of ROLANDO and "*v*," it was found that the tongue was actively retracted and also directed towards the side of excitation.

ANATOMY.

The excitable region of the cortex which we have investigated in this research comprises about the lower third of the ascending frontal and parietal convolutions and the commencement of the supramarginal gyrus. More exactly, the area now under consideration is bounded below by the fissure of SYLVIUS, in front by the vertical limb of the præcentral sulcus, and by a line drawn from the inferior end of this latter vertically down to the Sylvian fissure, behind by a line drawn from a point just behind the anterior end of the intraparietal sulcus vertically downwards to the Sylvian fissure; and superiorly by a line drawn horizontally across the ascending frontal convolution on a level with the upper extremity of the præcentral sulcus above the bend in the fissure of ROLANDO, called the genu (inferior genu), and by a line drawn across the ascending parietal convolution from the genu of the fissure of ROLANDO to the anterior end of the intraparietal sulcus.

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* 'Ueber die Funktionen der Grosshirnrinde. Gesammelte Mittheilungen,' 2te Auflage, 1890, p. 53, also 'Real-Encyclopädie d. Gesammten Heilkunde.'

† 'Phil. Trans.,' 1888 (paper read February, 1887). For certain minute details see also SCHÄFER, 'Ueber die Motorischen Rinden-Centren des Affen-Gehirns,' Festgabe z. CARL LUDWIG gewidmet, 1887.

In our paper ('Phil. Trans.,' B., 28, 1888) on the minuter representation of the movements of the limbs, we have described and figured the anatomy of the excitable region, with a minor exception, which we must now notice. It will at the same time, perhaps, be useful to enumerate the chief points before described. Reference, moreover, to fig. 1 (Plate 8) will render this more easy.

The mode of termination and form of the fissure of ROLANDO we have elsewhere[*] fully described, and need, therefore, only allude to the inferior genu, as showing the position of the borderland between the areas for representation of the upper limb and of the face.

The præcentral sulcus we have fully described in our first paper in the 'Philosophical Transactions,'[*] but we would here refer to two small sulci in the ascending frontal and parietal convolutions respectively. In the ascending frontal convolution, at its lower part, there is a small vertical sulcus, *st* in fig. 1, about 3 millims. long, the lower end of which is about 4 millims. from the fissure of SYLVIUS, and it is situated about 8 millims. behind the præcentral sulcus and 5 millims. in front of the fissure of ROLANDO. This sulcus, which is very constant in *Macacus sinicus*, was figured in a previous paper[†] of ours as "*v*," and was described by SEMON and HORSLEY[‡] as forming the posterior border of the area for the more absolute representation of the vocal cords. In the ascending parietal convolutions there is also a slightly marked sulcus, *rct* in fig. 1, about 2 millims. long, situated vertically about 2 millims. behind the fissure of ROLANDO, and the same distance above the fissure of SYLVIUS and below the anterior end of the intraparietal sulcus. This small sulcus, which is not so constant as the sulcus "*v*," we propose to call "*u*."

These two small subordinate sulci are termed by EBERSTALLER, in Man, the sulcus transversus frontalis inferior and the sulcus retrocentralis transversus respectively.

We are inclined to adopt this nomenclature for the lower Monkey also. The point is specially discussed by Professor CUNNINGHAM in his memoir "A Contribution to the Surface Anatomy of the Cerebral Hemispheres" (Royal Irish Academy, Dublin, 1892).

---

[*] 'Phil. Trans.,' vol. 178 (1887), B, 6, p. 154.

[†] 'Phil. Trans.,' vol. 179 (1888), B, p. 206.

[‡] 'Phil. Trans.,' vol. 181 (1890), B, p. 197.

METHOD OF INVESTIGATION, INCLUDING NOTATION.

Operation and Method of Recording.—In all cases we have exposed the cortex cerebri, with the precautions against cooling, drying, &c., described in our previous papers. After the opening of the dura mater the sulci were, as before, carefully plotted out with fine compasses on paper, ruled mathematically with squares whose sides measured 2 millims. In this way, as before said, we obtained a projection of the configuration of the cortex, the surface of which was thus already divided into squares of 4 square millims. in extent (see Plate 8, fig. 2), an arbitrary number being given to denote each square; these were successively stimulated, and the result recorded. Throughout this paper we shall refer, as before, to these units of localisation as "squares."

In every case the anæsthetic employed was ether, and the animal was killed before it recovered from the narcosis.

Method of Excitation.—The excitation, as before, was applied by fine platinum electrodes 2 millims. apart and furnished from the secondary coil of a DU BOIS-REYMOND inductorium served by a one-litre bichromate cell. The strength of the faradic current used was very weak, the distance of the secondary coil varying from 12 to a maximum of 9 centims. Momentary application of the electrodes was also resorted to for the detection of the initial contraction. For the complete development of any movement, and at the same time ensuring against the incidence of epilepsy, we found that usually 2 seconds was a sufficient duration for the stimulus.

Arrangement of the Results Obtained.—Even with every effort to obtain an animal of the same size and age and of the same variety, it is nevertheless impossible to avoid certain minute differences which render difficult the direct transference of the facts relating to one square in one animal to another square in another experiment.

We combined the results of our twenty experiments in the following manner, and from control observations subsequently carried out are sure that our procedure has not involved any serious error.

Mode of Notation.—As in each experiment we had made exact drawings of the sulci on the ruled paper (see fig. 2), it was easy to denominate the horizontal lines of squares in successive order from the fissure of SYLVIUS by capital letters, viz.:— A, B, C, D, E, &c. (see fig. 2), whereas the vertical rows were designated by italic letters *a*, *b*, *c*, *d*, *e*, &c., commencing opposite the præcentral sulcus and proceeding from front to back.

In this way any given square could be at once fixed and spoken of, for example, as A*d*, F*e*, &c. When thus in possession of a general classification the *average* position and inclination of the sulci could be discovered and pricked off.

By this means we constructed fig. 2, in which is correctly given the *average* position of the sulci and size of the gyri in all the cases observed by us.

Having therefore before us the average configuration of the area under discussion and having denominated the squares subdividing it as above stated, the aggregation and collocation of the individual observations in each experiment became a very easy matter, since for any given portion of the surface explored the result of excitation in each animal was placed under the same heading.

To guard against the fallacy of producing a state of hyper-excitability in any one direction and to check our results containing the arrangement of representation, *i.e.*, whether vertical, or lateral, we moved the electrodes in different experiments sometimes vertically from square to square, at other times horizontally.

PRELIMINARY CONSIDERATIONS.

Before giving a detailed account of the results obtained in these experiments, it will be advisable to say a few words about the phenomenon of bilateral representation.

Bilateral Representation.—In a previous paper* by us on the excitable fibres of the internal capsule the question of bilateral representation was discussed. The views of BROADBENT were there referred to, viz. :—that bilateral movement was effected by impulses passing from the sound hemisphere across commissural fibres postulated to exist between the lower (*i.e.*, bulbo-spinal) centres of the two sides ; we gave also a list of movements credited as being bilaterally represented. As this question is so important, we have reproduced this list (see Table), and desire to comment further upon it.

TABLE 1.—Credited as Bilateral.

Movements of trunk muscles, *i.e.*, rectus abdominis	Class I. Not bilaterally represented.
Certain movements of tongue	
Conjugate deviation of eyes	
Turning of head	
Retraction of angle of mouth	Class II. Imperfectly bilaterally represented.
Pursing of lips	
Opening of eyelids	
Closing of eyelids	
Opening mouth	
Elevation of soft palate	
Pouting of lips	Class III. Truly bilaterally represented.
Mastication	
Swallowing	
Adduction of vocal cords	

In our previous paper on the Internal Capsule we showed that movements of a special character and which we have placed in Class I. being elicited from only a definite part of the cortex, could not be regarded as being bilaterally represented, *i.e.*, as being represented in both hemispheres, and being evoked by excitation of either hemisphere. Consequently, for these movements, no substitution of function by the opposite side of the brain is conceivable.

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* 'Phil. Trans.,' vol. 181 (1890), B, p. 73.

We desire now to say a few words respecting the present use of the term, bilateral movement, and also the term, bilaterally associated movement. As regards *bilateral movement* we believe we are right in stating that the general use of this term at the present time is partly the same as that of bilaterally associated movement, but this second term premises that there is an association between the representations in the nervous system of so-called bilaterally associated movements. We venture to think that the term bilateral movement should be strictly confined to its simplest meaning, viz., that in the execution of any definite muscular action or movement the muscles of both sides of the body are involved, though not necessarily to the same extent, or that the muscles acting are of the same name. We would urge that, physiologically speaking, the term bilateral movement can only mean simultaneous action of muscles on both sides of the body, and ought not to be used for the representation of those muscles in the nerve centres. We believe that a certain degree of laxity in the use of this expression has crept in by the employment of the word "associated." The term association connotes physiological co-operation and arrangement in the nervous system, *i.e.*, motor representation when the term is applied to movements. With this view the expression "bilaterally associated movement" has been frequently used to characterise the activity of the trunk muscles. We showed in our Internal Capsule paper that this was not justified by the facts, since the somatic or trunk muscles are as unilaterally represented, with the exceptions denoted in Table I., as are the limb muscles. This point has been treated of late by SHERRINGTON,* who has since shown that even the sphincter ani is unilaterally represented. Whatever may be the physical condition, *i.e.*, movements of different muscles for the performance of definite acts, there does not seem to be any ground for assuming, as has been so frequently done, that certain muscles, *e.g.*, those of the trunk, act in association, or that they are, therefore, bilaterally represented.

Apart from the special physiological interest attaching to this question of bilaterality, it is impossible for neurologists to correctly appreciate the pathology of epilepsy or the restoration of function when certain districts of the cerebral hemisphere have been destroyed until this question has been settled.

ANALYSIS OF RESULTS.

We have arranged the movements elicited by excitation of the region observed according to the following classification.

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* 'Journal of Physiology,' 1892.

I. ORIFACIAL Movements.

A. Face	(a) Upper face	(1) Eyelids	Opposite side	Closing
			Bilateral	Opening
		(2) Eyes	Conjugate deviation to the opposite side	Opposite side
		(3) Angle of mouth	Elevation of	Same side
	(b) Lips	(1) Upper lip	Inversion	Opposite side
		(2) Lower lip	Eversion	Same side
				Bilateral
	(c) Lower face	(1) Angle of mouth	Retraction of	Opposite side
				Same side
				Bilateral
		(2) Angle of mouth	Advancing of	Opposite side
				Same side
				Bilateral
		(3) Pursing of mouth		
		(4) Pouting of mouth		
		(5) Cheek		
		(6) Chin		
B. Tongue		(1) Movements towards the opposite side		
		(2) Movements towards the same side		
		(3) Bilateral movements		
C. Lower jaw		(1) Single movements	Lateral	
			Vertical	
		(2) Rhythmical movements	Mastication	
D. Pharynx		(1) Soft palate (elevation of)	Opposite side	
			Same side	
			Bilateral	
		(2) Swallowing		

II. MOVEMENTS otherwise than Orifacial.

A. Head.
B. Upper Limb.

We will now take the movements observed in the present research, seriatim, and give in detail first the squares in which they are represented, arranging these in the order of greatest frequency of occurrence of the movement. Under the same heading we shall treat of the individual points of importance and interest observed for each movement.

I. ORIFACIAL MOVEMENTS.

A. *Face.*

(*a.*) *Upper Face.*

(1.) *Representation of the Movements of the Eyelids.*

(*a.*) Closure	Opposite eyelids. Eyelids of both sides.
(*b.*) Opening	Eyelids of both sides.

(*a.*) *Closure of Opposite Eyelids* (fig. 3).—This movement, which possesses a well-defined focus of representation in the Monkey's cortex, corresponds to that seen in the cortex of the Dog (*vide* FRITSCH and HITZIG, FERRIER, LUCIANI, PANETH, and others).

Closure of the opposite eyelids was noted by us to occur at the following squares in the order of greatest frequency, as shown by the numbers :—

6.	5.	4.	3.	2.	1.			
Hj	Fj Gj	Fi Gi Ig	Fk Fl Ii	Ih	Ek El Em	Fm Gk Hl Hk	If Jf Ji Jj	Kf Kg Kh Ki

It will be understood that excitation of these points elicited only closure of the pair of eyelids of the opposite side to that of the hemisphere stimulated. It is very well shown to be unilateral in instantaneous (flash) photographs taken during excitation. We only once observed bilateral action, viz., closure of both pairs of eyelids at Gj.

There is in addition a very characteristic bilateral movement of the eyelids (*i.e.*, both pairs), popularly termed blinking, which requires description. This consists of a rhythmical closure, or opening of both pairs of eyelids. This is, of course, quite different to the movement just mentioned. We observed it to occur in three separate experiments upon excitation of the square Fj.

(*b.*) *Opening of the Eyelids of Both Sides.*—This movement we do not regard as being specially represented in the area under discussion (*i.e.*, posterior to the sulcus præcentralis, inferior and anterior to the lower end of the intraparietal sulcus), because, as has been shown by other investigators besides ourselves, the focus of this movement is situated in front of the præcentral sulcus. We noted it, however, to occur once at Ie in an animal in which the ascending frontal gyrus was exceptionally broad.

(2.) *Representation of the Movements of the Eyes.*

(*a.*) *Conjugate Deviation of the Eyeballs to the Opposite Side to that of Excitation.*—This well-known movement, the chief focus of which is situated in front of the præcentral sulcus, we elicited from the squares—

2.	1.
Gl	El Fm

These squares, it will be seen, are situated at the commencement of the supramarginal gyrus, or, as it is often improperly termed, the anterior limb of the angular gyrus, wherein this movement has previously so often been observed to be represented (*vide* FERRIER, LUCIANI, SCHÄFER).

We observed no other movements of the eyeballs.

(3.) *Angle of Mouth, Elevation of.*

We subdivide the representation of the movement of elevation of the angle of the mouth under the following headings :—

(*a.*) Elevation of the opposite angle of the mouth.
(*b.*) Elevation of the angle of the same side.
(*c.*) Elevation of both the angles of the mouth.

(*a.*) *Elevation of the Angle of the Opposite Side* (fig. 4).—This, by far the most frequent movement of elevation, was observed at the following large number of squares :—

7.	6.	5.	4.	3.	2.	1.
G*g* G*h*	E*j* G*f* G*i* H*h* I*g*	E*k* F*g* H*g*	D*k* H*f* E*i* I*h* F*h* F*j* F*k*	E*g* F*f* F*i* G*j* H*j* I*f*	D*i* D*j* E*h* E*l* F*l* G*e*	C*h* E*e* J*f* C*i* E*f* J*g* C*j* F*d* J*h* C*k* G*d* D*e* H*k* D*l* I*i*

As is seen in fig. 4 the focus of greatest representation is at G*g*, G*h*.

(*b.*) *Elevation of the Angle of the Same Side.*—The representation of this movement, which from *à priori* considerations we did not anticipate finding, was observed in single instances at squares :—

A*f* B*j* C*j* D*i* F*h*.

(*c.*) *Elevation of both the Angles of the Mouth.*—As a corollary to the facts just related, the actual observation of bilateral representation of this movement of elevation of the angle of the mouth was seen on two single occasions, viz., at squares—

C*l* C*e*.

This bilaterality is therefore very rare.

(*b.*) *Lips.*

In describing the movements of the lips we have observed occasionally such unilaterality of representation as to lead us to regard the lips, *e.g.*, the upper and the lower, as divisible into two halves, viz., the right and the left. We have, therefore, subdivided the lips into four regions, a right and left upper and lower lip. We thus classify the movements noted, according as to whether they affect the upper or lower lip individually, and further whether it is of the opposite or of the same side, or whether both sides move at once. The movements observed are as follows :—

(*a.*) Elevation of the upper lip of the opposite side.
(*b.*) Depression of the lower lip of the opposite side.
(*c.*) Inversion of the lower lip of the opposite side.
(*d.*) Inversion of both lips of the same side.
(*e.*) Inversion of both lips of both sides, but especially of the opposite side.
(*f.*) Inversion of both lips.

(*a.*) *Elevation of the Upper Lip of the Opposite Side.*—This is a rare movement of remarkably unilateral character which differs from simple elevation of the angle of the mouth in that the ala of the nose is not moved. It was observed to occur only once at squares B*j*, C*f*, and C*g*.

(*b.*) *Depression of the Lower Lip of the Opposite Side* (fig. 5).—This movement is represented at the following squares :—

3.	2.	1.	
F*g*	Fe	F*h*	I*i*
I*g*	G*g*	G*d*	J*f*
	H*g*	G*e*	J*g*
	I*f*	G*f*	
	I*h*		

(*c.*) *Inversion of the Opposite Lower Lip.*—This, as a solitary movement, occurred only once at G*l*.

(*d.*) *Inversion of both Lips of the Same Side.*—This occurred twice at E*h*.

(*e.*) *Inversion of both Lips of Both Sides, but especially the Halves of the Opposite Side.*—In this case the whole length of the upper and lower lips was inverted, but the opposite halves were affected notably more than those of the same side. The movement was found at squares—

2.	1.			
F*e*	A*f*	E*c*	F*f*	H*e*
F*j*		E*d*	F*k*	H*f*
G*i*		E*e*	G*e*	H*j*
G*j*		E*i*		H*k*
G*k*		E*j*		H*l*
I*f*		E*k*		

(*f.*) *Inversion of Upper and Lower Lip of Both Sides.*—This movement is similar to the one just described, except that it was completely bilateral, no difference being found between the two sides. It occurred once at A*g*, B*f*, B*g*, B*h*, B*i*, B*j*, D*i*, D*k*, E*h*.

(*c.*) *Lower Face.*

We now come to the movements of the lower part of the face and commence with those of the angle of the mouth. These may be suitably arranged as follows :—

(*a.*) Retraction of the angle of the Mouth of the opposite side.
(*b.*) ,, ,, ,, ,, ,, ,, same side.
(*c.*) ,, ,, ,, ,, ,, both sides.
(*d.*) Advancing ,, ,, ,, ,, the opposite side.
(*e.*) ,, ,, ,, ,, ,, ,, same side alone.
(*f.*) ,, ,, ,, ,, ,, both sides.
(*g.*) ,, ,, ,, ,, ,, the same side together with the cheek.
(*h.*) Depression ,, ,, ,, ,, ,, ,, ,, ,,

(*a.*) *Retraction of the Angle of the Mouth of the Opposite Side* (Plate 8, fig. 6).—This, with that of elevation of the angle of the mouth, is the most important movement of the face, and has long been recognized to be so. In the movement of retraction, the angle of the mouth is drawn horizontally backwards without necessarily parting the lips. It occurred at squares—

12.	9.	8.	7.	6.	5.	4.	3.	2.	1.
D*j*	E*j* H*g*	E*k* H*h*	E*g* E*i* F*i* F*j* G*g*	D*k* F*g* H*f*	C*j* D*i* G*f* H*j*	D*f* F*e* F*f* F*h* G*h* G*j* I*e* I*g*	C*h* C*k* D*l* E*h* F*k* G*i* G*k* G*l* I*h*	B*g* B*i* B*j* D*h* E*e* E*f* F*m* H*l* J*f* J*g*	B*h* C*f* C*g* C*h* D*g* E*d* E*l* F*l* G*d* G*e* H*k* J*h*

(*b.*) *Retraction of the Angle of the Mouth of the Same Side.*—Particular notice must be taken of this movement as it occurs on the *same* side as that of the hemisphere excited. It was found in squares—

2.	1.		
A*f* B*f* B*g*	A*g* A*i*	B*i* C*b* D*f*	E*g* G*h*

Its relative infrequency is very obvious.

(*c.*) *Retraction of the Angle of the Mouth of Both Sides* (fig. 7).—This truly bilateral movement was seen at squares—

3.	2.	1.		
C*j*	C*i*	C*g*	D*g*	D*k*
C*k*	E*f*	C*h*	D*i*	D*l*
	E*g*	D*c*	D*j*	F*f*

The next kind of movement which we noticed to affect the angle of the mouth was in the opposite direction to that just mentioned of retraction, and may properly be described as advancing. In this the angle of the mouth is drawn or pushed forward, and the movement may occur on either the side opposite to that of the hemisphere excited, or on the same side, or bilaterally, *i.e.*, both angles of the mouth are advanced simultaneously, and, as will be subsequently seen, also accompanied by movement of the cheek.

(*d.*) *Advancing of the Angle of the Mouth of the Opposite Side.*—This, the crossed unilateral action as generally understood, we only noted to occur in single instances at

D*h* G*e* G*g* G*h* H*f* H*g*.

(*e.*) *Advancing of the Angle of the Mouth of the Same Side Alone.*—This rare movement was observed only once at D*h*.

(*f.*) *Advancing of the Angle of the Mouth of Both Sides.*—This, which is a well-marked bilateral movement, is in our opinion the forerunner to the important movements of pouting and pursing of the mouth. We observed it repeatedly at squares, viz.:—

3.	2.	1.			
F*g*	D*h*	B*e*	D*d*	D*f*	D*k*
	G*f*	C*f*	D*e*	D*g*	G*h*

(*g.*) *Advancing of the Angle of the Mouth of the Same Side together with the Cheek.* This combined action of the forward movement of the angle of the mouth and cheek was only observed twice at C*h*, and must be looked upon as an exceptional development of the advancing of the angle of the mouth.

(*h.*) *Depression of the Angle of the Mouth* (*i.e.*, *Platysma Action*).—We only observed this movement to occur twice, viz., at centres C*g* and C*h*.

(3) *and* (4). *Pursing and Pouting.*[*]

There remain for consideration certain combined actions of the lips and orifice of the mouth which are easily recognized under the quasi-popular expressions of pursing and pouting, but which cannot be described sufficiently accurately except by long periphrasis. To avoid this we employ the former expressions under the following meanings.

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[*] 'Phil. Trans.,' B, 1890, p. 136.

Pursing.—By this term, as we have already described in our paper on the motor cortex of the Orang,[*] we mean the drawing together of the lips, together with slight protrusion, both parts of the orbicularis being contracted, whilst in *Pouting* the lips are strongly protruded, and at the same time they are much everted.

We may subdivide this subject in the following manner :—

(*a*.) Pursing of the opposite side of the mouth.
(*b*.) Pursing of both sides of the mouth (bilateral).
(*c*.) Pouting of the opposite side of the mouth.
(*d*.) Pouting of the same side of the mouth.
(*e*.) Pouting of both sides of the mouth.

(*a*.) Pursing of the opposite side of the mouth was only observed once at the squares E*c*, E*d*, E*e*, I*g*.

(*b*.) Pursing of both sides of the mouth occurred at—

2.	1.		
E*g*	E*h*	F*h*	G*f*
F*g*	Fe	F*k*	He
H*f*	F*f*	Ge	H*g*

(*c*.) Pouting of the opposite side occurred at—

3.		2.	1.	
D*i*	D*j*	E*e*	E*c*	F*d*

(*d*.) Pouting of the same side of the mouth occurred only once at D*h*

(*e*.) Pouting of both sides of the mouth was seen at—

3.	2.		1.				
F*h*	B*e*	E*f*	A*d*	B*f*	C*h*	Fe	G*h*
	C*e*	F*f*	B*b*	C*b*	E*g*	F*g*	
	D*i*	G*g*	B*d*	C*c*	E*h*	G*f*	

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[*] 'Phil. Trans.,' B, 1890, p. 136.

(5.) *Movements of the Cheek.*

In close relation with the movements of the angle of the mouth are those of the cheek, which may be divided into the two following groups :—

(*a.*) Flattening of the cheek on the same side.
(*b.*) Flattening of both cheeks.

(*a.*) *Flattening of the Cheek on the Same Side* (fig. 8).—This movement was found at the following squares :—

4.	3.	2.	1.	
D*g*	D*h*	B*g*	B*d*	E*d*
C*f*		C*g*	B*f*	
		E*h*	D*f*	G*g*
		G*h*		
		E*f*		
		E*g*		

And it was seen to be almost invariably associated with a special movement of the tongue, viz.: rolling over of the dorsum to the cheek of the same side (p. 55), so that the cheek moved to meet the dorsum of the tongue, and would thus force, and keep the bolus of food between the molar teeth.

It is interesting to note that this movement occurred as a unilateral action and only on the same side as that of the cortex stimulated.

(*b.*) Bilateral flattening of the cheeks occurred only as a single instance at E*h*. It is, therefore, very exceptional.

(6.) *Movements of the Chin.*

The movements of the chin are the last we have to note, of those observed in the lower face.

They may be considered under the heads of—

(*a.*) Elevation of the chin on the opposite side.
(*b.*) Elevation of the chin on the same side.
(*c.*) Bilateral elevation of the chin.

(*a.*) *Elevation of the Chin on the Opposite Side.*—This is by far the commonest movement of the chin met with, and is probably caused by the levator menti muscle. It occurred at—

2.	1.			
D*i*	C*h*	D*g*	D*k*	F*h*
E*j*	C*i*	D*h*	E*i*	F*k*
E*k*	C*j*	D*j*	E*l*	

(*b.*) *Elevation of the Chin on the Same Side.*—This was very rare and occurred as a single observation at E*g*.

(*c.*) *Bilateral Elevation of the Chin.*—This occurred only once at squares C*h*, E*h*.

B. *Movements of the Tongue* (Plate 9, fig. 9).

The question of the manner in which the various movements of the tongue should be grouped was alluded to in the consideration of bilateral representation on p. 44. We have decided to divide the movements of the tongue into—

1. Movements bilaterally represented.
2. Movements not bilaterally represented.

They may therefore be arranged in the following order :—

1. Movements bilaterally represented.
   - (1.) Tongue protruded straight.
   - (2.) Tongue retracted straight.
2. Movements not bilaterally represented.
   - (1.) Tongue protruded, tip to the opposite side.
   - (2.) Tongue protruded to the same side.
   - (3.) Tongue retracted on the same side.
   - (4.) Tongue rolled over with the dorsum to the cheek of the same side.

1. *Movements Bilaterally Represented.*

(1.) *Tongue Protruded Straight* (Plate 9, fig. 10).—This simple bilaterally represented movement, *i.e.*, which can be evoked equally well from the cortex of either hemisphere, was found at the following squares :—

6.	5.	4.	3.	2.	1.
A*e* B*f* C*e*	B*e* C*d*	A*b*	A*c* A*d* A*f* A*g* C*f* D*d* D*e*	B*g* C*c* C*g* C*j* D*g*	A*b* B*d* B*c* B*d* C*b* C*i* C*k* D*c* D*f* E*i* F*i*

In this movement the tongue is protruded quite flatly and without any deviation of the tip to one side, and without any heaping up posteriorly.

(2.) *Tongue Retracted Straight.*—This was less widely represented than the former, and was found at—

3.	2.	1.		
B*h*	B*g*	C*c*	D*e*	G*h*
C*e*	B*i*	C*h*	D*h*	
		C*j*	D*j*	

2. *Movements not Bilaterally Represented.*

(1.) *Tongue Protruded with the Tip to the Opposite Side* (fig. 11).—This is the movement upon which so much stress has been laid in clinical observation, and the real nature of which will further on be more minutely discussed. It was found to be represented at squares—

4.	3.	2.					1.					
D*f*	B*i*	A*i*	C*k*	D*k*	E*k*	G*g*	B*b*	C*g*	E*c*	F*f*	G*j*	I*h*
E*g*	C*i*	B*e*	D*e*	E*e*	F*i*	G*h*	B*c*	C*h*	E*d*	F*h*	H*f*	J*e*
	D*j*	B*g*	D*g*	E*h*	F*g*	H*e*	B*d*	D*d*	E*l*	F*j*	I*e*	J*f*
	E*i*	C*f*	D*i*	E*j*	G*e*	H*h*	B*h*	D*h*	F*d*	G*d*	I*f*	J*g*
	H*g*	C*j*					C*e*	D*l*	F*e*	G*f*	I*g*	

(2.) *Tongue Protruded with the Tip to the Same Side.*—This movement, in marked contrast to the former one, was obtained three times at only one square, A*f*.

(3.) *Tongue Retracted on the Same Side.*—This movement, which is very slightly represented, was found once at G*g*.

(4.) *Tongue Rolled over so that the Dorsum comes into contact with the Cheek of the Same Side* (fig. 12, *cf.* fig. 8).—This movement is one in which there is no protrusion of the organ, but in which it is so rotated on its longitudinal axis that the dorsum of the tongue is closely applied to the mucous membrane of the cheek of the same side as that of the cortex stimulated. As previously stated, the cheek of the same side is flattened to meet the convexity of the approaching tongue. It occurred at—

5.	4.	3.	2.	1.		
B*g*	C*g*	D*f*	A*h*	B*f*	D*e*	E*k*
	C*h*	D*g*	B*h*	C*b*	E*g*	F*g*
	D*h*		C*e*	C*f*	E*h*	
			E*f*	C*i*	E*i*	
			F*h*	C*j*	E*j*	

Consideration of the foregoing Facts with especial Reference to Movements of the Individual Halves of the Tongue after Separation along the Median Plane.

We have already described the movements of the tongue as a whole, and we have alluded to the questions of unilaterality and bilaterality of movement of this organ. A new and unexpected light was thrown on this subject by the following attempt to differentiate the complex movements of the entire tongue, and to determine what share is taken by each half in the production of any given action.

It occurred to us that much might be learnt by regarding the tongue, at least for the longitudinal muscles, as constructed of two similar halves; further, that these might be separated from each other by a vertical incision in the middle line, and this without injury to the nerve supply of each half.

Of course we recognize that this procedure involves the median* division of the septal origin of the transverse muscular fibres and also the division of any hypothetical nerve fibres crossing the raphe, but this does not invalidate the results we obtained, and which show most definitely that the movements of both halves of the tongue are represented in the hemisphere of each side respectively. For illustration of our meaning, and for the better comprehension of the facts about to be related, we may compare the question of this bilateral representation of the movements of the respective halves of the tongue with those of the conjugate movements of the eyes, and it will be seen presently that the common, and in hemiplegia previously supposed unilateral, movement of the tongue is really a conjugate movement.

The operation of separation was performed by dividing the tongue along the median plane from the hyoid bone and root of the epiglottis forward to the genial tubercles. As a rule there was exceedingly little hæmorrhage, and this was easily arrested by pressure. The reflex movements of the tongue were as complete as before, showing that the functions of the organ were not interfered with.

We will now take the movements of the tongue as a whole (see p. 54), and discuss in the light obtained by this method how far the change of form of the whole organ is dependent on each of the halves respectively; we will therefore take the movements in the same order in which they have just been considered.

Movements Bilaterally Represented.

(1.) *and* (2.) *Advancing and Retraction of the Tongue.*—We observed that in these movements executed symmetrically forwards or backwards, each half of the tongue performed exactly the same evolution, and in no case could preponderance of action be shown to take place on either side. It follows therefore that these movements are truly bilaterally represented.

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* Practically the line of separation frequently passed close to the side of the septum, this, of course, not interfering with the power of the transverse fibres to contract, and so narrow the half of the tongue.

Movements not Bilaterally Represented.

(1.) *Protrusion of the Tongue to the opposite side.*—From the time of ABERCROMBIE[*] it has been noticed in clinical medicine that in hemiplegia the tongue was protruded towards the paralyzed side, *i.e.*, opposite to the lesion, and this was assumed to be due to the genio-hyo-glossus muscle of the healthy side (*i.e.*, the same as the lesion) pressing the tongue towards the paralyzed side, *i.e.*, away from the lesion.

In CARPENTER's Physiology[†] it is stated that the deviation is due to the want of action of the lingual muscles of the paralyzed side, the tip being directed by the muscles of the other (*i.e.*, healthy) side, "which will not act in a straight direction when not antagonized by their fellows."

In short, it is evident that a general belief exists to the effect that if one side of the tongue is being actively protruded, the other half remaining passive the resulting position of the tongue is a deviation towards the paralyzed side owing to the passive flaccid condition of the non-acting muscles. The first point which we think requires to be definitely ascertained in treating this subject is the determination as to whether excitation of *one* hypo-glossal nerve produces any movement of the tongue across the median plane, as is evidently generally supposed. We ourselves having foreseen the complex problems involved in the movements of this part especially re-investigated, by excitation experiments at the base of the skull, the functions of several cranial nerves separated from the medulla. We found ('Roy. Soc. Proc.,' vol. 44, June 7, 1888) that excitation of the hypo-glossal nerve of one side produced in the whole tongue "flattening posteriorly on the same side and the tip protruded also on the same side." The purely unilateral character of the movement was further established by experiments in which the tongue was divided longitudinally to the hyoid bone when the movements were seen to be entirely confined to the side stimulated.

It will therefore be seen that stimulation of the hypo-glossal nerve of one side does not protrude the tongue towards the opposite side.

We will now proceed to describe what happens to the individual parts of the tongue when in the left cortex the squares for the representation of protrusion of the tongue to the opposite side are excited. Instead of the right half of the tongue remaining passive as has always been presupposed by anatomists and clinicians, we discovered that when the left cortex was stimulated the following remarkable conjugate movement occurred :—the left half of the tongue was advanced beyond the teeth, whereas the right half was actively retracted into the mouth. It is perfectly obvious therefore, that this movement of protrusion of the tongue to the opposite side from stimulation of the cortex is exactly comparable to the conjugate movement of the eyes to the opposite side when the same hemisphere is excited. In this way the right half of the tongue would correspond to the right external rectus, and the left half of the tongue to the left internal rectus. In each case we have the combination of two opposite movements for the production of one resultant action. The opposite character of the movements of the two halves of the tongue was emphasized in a very remarkable degree when there was epileptic disturbance of the cortical focus in question. In the clonic spasm of the epileptic fit the two halves performed remarkable "see-saw" contractions, that of the same side being shot forwards at the same time as the opposite half was retracted. On several occasions we observed that retraction of the opposite side not only began before the protrusion of the same side, but actually in a few instances it occurred alone, thus showing that it is probably the more important movement of the two. We are now in a position to examine into the condition of the tongue as observed in hemiplegia. Unfortunately the clinical examination of the tongue has hitherto not been conducted so thoroughly as its importance warrants; and in fact, clinical observation is usually limited to noticing whether the tongue is deviated to one side when protruded, without further exploration of other movements. This is doubtless due to the fact that the movements of the tongue generally have hitherto not been completely ascertained. Although this makes the task of explanation very difficult and for the present impossible, we take leave to point out that the accepted views are plainly contrary to fact and will have to be altered.

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[*] 'Pathological and Practical Researches on Diseases of the Brain and Spinal Cord,' Edinburgh, 1834, p. 271.

[†] CARPENTER's 'Physiology' edited by POWER, 7th edition, 1869. Compare also ROSS' 'Treatise on Diseases of the Nervous System,' 1883, and GOWER's 'Diseases of the Nervous System,' 1888.

(2.) *Rolling over with the Dorsum directed towards the Cheek of the Same Side.*—This movement we found to be distinctly compound in character, both separated halves of the tongue rolling to the same side. In the execution of this movement the mucous membrane of each half of the tongue was turned so as to be directed towards the left cheek, as a result the cut surfaces glided upon each other so that the two halves were arranged *en échelon* in place of being in line; the cut surface of the same side being directed upwards and that of the opposite side downwards.

Each half of the tongue therefore executes a rotation around its longitudinal axis.

Vertical Arrangement of the Representation of the Movements of the Tongue.

Reference to the diagrams (Plate 9, fig. 9, &c.) will show that a very definite differentiation of the representation of the tongue movements can be made as follows. In the upper part of the area, *i.e.*, just below a line drawn between the upper end of the præcentral vertical stem and the genu of the fissure of Rolando, the action of protrusion of the tongue with the tip directed to the opposite side is elicited on excitation. On the contrary, the movement of retraction is represented at the lowest portion of the area, *i.e.*, around the lower end of the fissure of Rolando. Intermediately, *i.e.*, opposite the upper end of the sulcus transversus frontalis inferior (see p. 42) we find the movement of rotation of the tongue towards the same side.

C. *Movements of the Lower Jaw.*

The movements of the lower jaw may be divided into :—

1. Single movements.
    (1.) Opening the mouth straight.
    (2.) Opening of the mouth with the lower jaw directed towards the same side.
    (3.) Opening of the mouth with the lower jaw directed towards the opposite side.
    (4.) Shutting the mouth.
2. Rhythmical.
    (1.) Mastication.

1. *Single Movements.*

By the term " opening the mouth " we understand that the lower jaw is depressed. This movement we have observed to occur without necessarily separating the lips, which additional passive action, however, nearly always happens concurrently. We therefore consider these two cases.

We look upon the movement as being accomplished by the muscles of both sides, but we have no evidence to show whether they act concurrently and whether the movement, if it does not deviate from the middle line, is capable of being produced by the muscles of one side only. It is known that if one external pterygoid muscle act alone, the jaw on being depressed is carried towards the opposite side, and we therefore assume that this occurs when the jaw deviates towards one side or the other.

(1.) *Opening the Mouth Straight* (fig. 13).—In this movement the jaw is depressed exactly straight along the line between the two central incisors. It was found at—

10.	9.	8.	7.	6.	5.	4.	3.	2.	1.
D*g*	A*f* A*g* B*f*	C*g* C*i*	B*g* B*i* C*e* C*h*	A*e* A*h* B*e* B*h* C*f* D*f* D*h*	C*j*	C*d* C*k* D*e* E*g*	A*b* A*d* A*i* B*d* B*j* C*c* D*d* G*g*	A*c* B*d* D*c* D*i* E*h* E*i* E*k* F*h* G*h*	B*c* C*l* D*j* D*k* E*f* E*j* H*g* H*l*

(2.) *Opening the Mouth with the Lower Jaw Carried to the Same Side* (fig. 14).—In this movement, with stimulation of the left hemisphere, the lower jaw as it descended moved markedly towards the left side ; this we take to be due to the fact that either the right pterygoid muscle alone was in action, or that it overpowered that of the left side. While as just seen the commonest movement of depressing the lower jaw in opening the mouth is the bilateral or straight movement, where any deviation was noticed, it was this one of the lower jaw passing to the same side as that of the cortex excited. This might have been anticipated from what has been stated, as it is obviously an instance of the ordinary crossed effect of stimulation. This movement occurred at—

4.	3.	2.		1.		
B*g*	C*g*	A*e*	D*h*	A*d*	B*h*	D*d*
D*g*		A*f*	E*h*	B*c*	C*b*	D*f*
		B*d*	E*j*	B*e*	C*f*	E*g*
		C*d*		B*j*	C*h*	

(3.) *Opening of the Mouth with the Lower Jaw carried to the Opposite Side.*—This, which is the converse of that described, and was very rarely observed, is conceivably due to the action of the external pterygoid muscle of the same side, and was obtained only once at two squares, A*d*, A*e*.

On looking at the previous Table it will be seen that the movement of the jaw towards the *same* side was also obtained twice at A*e* and once at A*d*, thus showing that there are squares where the differentiation of the movement of the lower jaw towards the opposite side was incomplete, its production being due, therefore, more or less to an accidental causation.

(4.) *Shutting of the Mouth.*—This well recognized movement of closing the mouth was, to our surprise, obtained at only one square, viz., D*h*. By this movement we mean simply raising up the depressed lower jaw, without any further action, and the very small representation of this deliberate act is in marked contrast to that of the rhythmical movements to be next described.

2. *Rhythmical Movements.*

(1) *Movements of Mastication* (fig. 15).—By the term "mastication" we mean that on the application of the electrodes to the cortex, the lower jaw begins to execute a series of rhythmical movements of grinding of the teeth. To describe the movement in detail:—the mouth is opened, the lower jaw depressed and carried towards the same side, and then the mouth is closed by raising the lower jaw; directly the teeth are separated the tongue is advanced, and it is retracted immediately before the teeth come together again; this latter movement of the tongue is thus dependent on and coincident with the action of the lower jaw. This complex act of mastication begins immediately the electrodes are applied, and continues until the electrodes are removed, when it ceases. The movement is what would generally be termed that of mastication of a very pronounced type, and as such it differs somewhat from the description given by Professor FERRIER, in that he does not seem to have observed the grinding movements of the lower jaw. The most important point concerning it is

that it is an instance of rhythmical discharge of the cortex evoked by a constant stimulus, and lasts only during the duration of the excitation. So far as we know, it is the only truly rhythmical action following on stimulation of the cortex.*

With a view to seeing what this rhythmical rate might be we observed the time of it in seventeen cases, and found it to be on an average 1·35 movements per second, the most rapid rate observed being nine times in five seconds, and the slowest being one in one second, and each of these extreme cases was noted three times.

This compound act was observed at—

8.	7	6.	5.	4.	3.	2.	1.
Be	B*d*	C*d*	Ae Bc Ce	A*b* A*d* B*f* C*f* D*d*	Ac A*f* B*g* Cc C*h* De D*f*	A*g* C*g* Dc D*g* E*f* E*g*	B*b* C*b* C*i* C*j* D*h* E*d* E*h* Fe F*f* F*h*

Grinding of the Teeth.—On three occasions the teeth were observed to grind during the act of mastication, and in two of these the movement of the jaw was traced and found to pass from the opposite side to the same side. The squares where it was observed were A*d*, Ae, A*f*.

Movements of the Pharynx.

In observing these movements, we kept the mouth forcibly opened, and recorded, as far as possible, the movement of, 1, the soft palate; and 2, that of swallowing.

1. *Movements of the Soft Palate* (fig. 16).

We may arrange the movements of the soft palate as follows :—

(1.) Elevation of the soft palate on the opposite side.

(2.) Bilateral elevation of the soft palate.

(3.) Bilateral elevation of the soft palate, commencing with elevation of the opposite side, followed later by that of the same side.

(1.) *Elevation of the Soft Palate on the Opposite Side.*—This movement of the soft palate, when viewed in the manner described, is quite unmistakable when it occurs; but it has to be carefully distinguished from the irregular movements of the arches of the fauces, when these are drawn forward by the tongue and by the movements of this organ itself. The movement was only observed once, at B*d*; and at the same place slight opening of the mouth and protrusion of the tongue to the opposite side were noted.

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* Compare as an imperfect rhythm the act of blinking, see p. 47.

(2.) *Bilateral Elevation of the Soft Palate.*—This movement, which is the commonly understood effect—viz., the raising of the whole soft palate—was seen only four times, viz., once at squares A*d*, A*e*, B*d*, C*d*. Of these at A*d*, B*d*, C*d*, this was the only movement obtained ; while at A*e* there was also the movement of mastication.

The foregoing refers to experiments in which the observation of the soft palate was made at the end of the exploration. It occurred to us that possibly the paucity of these results was due to exhaustion of the cortex. We therefore devoted two experiments to examine this point first, with the effect that we obtained very definite localisation of the palate movements.

(1.) ELEVATION of the Soft Palate on the opposite side.

2.	1.
B*f* C*f*	A*d* A*e* A*f* B*d* B*e* C*d* C*e*

(2.) BILATERAL Elevation of the Soft Palate.

1.
A*e* B*c* B*e* C*e*

(3.) BILATERAL Elevation commencing with elevation of the opposite side, followed later by that of the same side.

1.
B*d* C*d*

These further observations showed clearly the real degree of representation of the palate, and in addition, what we did not anticipate, namely, a considerable degree of unilaterality of representation.

2. *Movement of Swallowing.*

This movement was observed once at four squares, viz.:—

Ad, *Ce*, *Cj*, *Df*.

The paucity of representation is perhaps accounted for by the movement of swallowing in the Monkey being more automatic than is generally considered to be the case, but it is possible that the effect of exposure may influence the result.

In relation to this question, the recent observations of GOLTZ,* in which he successfully removed both cerebral hemispheres in the Dog, leaving only the cerebellum, pons, bulb, and posterior corpora quadrigemina intact (the anterior partially so), and kept the animal alive for many months, must be specially mentioned. The animal had to have milk poured down its throat through a tube, because the act of swallowing was so far interfered with that fluid almost always escaped into the larynx. In two months after the operation, it would, when its nose was touched with a piece of meat, seize it, masticate it, and swallow it without any assistance. There seems, therefore, on the whole, to be no real reason why in the Monkey the cortical representation of swallowing should be more extensive than such as we find it to be.

II. MOVEMENTS OTHERWISE THAN ORIFACIAL.

In exciting the area under examination, since we were devoting ourselves especially to the orifacial movements, we only noted the concurrence of movements of other parts of the body when those appeared to us anomalous, and in order to satisfy ourselves of the extent of such extra movements, and to control the observations which we made in 1886, and also to ascertain to what extent the orifacial area overlapped the neighbouring areas.

The movements thus noted comprised those of the head and of the upper limb.

A. *Movements of the Head.*

Since the region which we have explored in the present research is in direct continuity with the supramarginal gyrus, and this with the anterior limit of the angular gyrus, it was to be anticipated that we should observe movements of the head and eyes to the opposite side, inasmuch as FERRIER, SCHÄFER, and others, observed these movements to occur from excitation of this region. The movements of the head which we noticed were (1) the turning of the head to the opposite side, and (2) retraction of the head.

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* 'Archiv für d. Gesammte Physiologie' (PFLÜGER), vol. 51, p. 570, 1892.

(1.) *Turning of the Head to the Opposite Side.*—This movement, where the head is turned away from the side of the cortex stimulated, was found at the following squares :—

4.	3.	2.		1.			
D*l*	C*l*	E*j*	G*k*	B*j*	E*k*	G*l*	J*f*
D*m*		F*k*	I*f*	C*k*	E*m*	H*m*	J*h*
		F*l*		D*j*	F*i*	I*e*	
		F*m*				I*g*	
						I*h*	

The representation of this act is, therefore, round the fringe of the orifacial representation, especially at the posterior part near to the supramarginal gyrus, and also at the upper part of the region where it borders on the area representative of this movement in front of the præcentral sulcus.

(2.) *Retraction of the Head.*—Similarly the rarer movement of retraction of the head was noted to occur once at each of the following squares :—C*j*, C*k*, D*h*, D*i*, E*j*, F*h*, F*i*, F*k*, I*g*.

B. *Movements of the Upper Limbs.*

Although we noted the various movements of the segments of the upper limb we did not record the occurrence of the same in the present work with detail, but we have made a considerable series of observations to re-investigate the question of overlapping, and the extent of border centres, and recorded also certain anomalies of representation. In the present instance we have specially noted the lowest points at which movements of the upper limb could be elicited. These when arranged give the following results, commencing with the thumb and fingers, which according to our observations, both in 1886 and in the recent experiments, are the lowest segments represented.

	In front of Rolando.						Behind Rolando, anomalous.			
Thumb	D*d*	D*e*	E*f*	E*g*	G*h*		H*j*	C*j*	C*k*	
Fingers	D*c*	D*d*	D*e*	E*f*	F*g*	G*h*	G*j*	E*k*	D*l*	D*m*

In contrast to these segments we give the lower limits of the representation of the elbow and shoulder, as found in the present experiments.

	In front of Rolando.	Behind Rolando, anomalous.
Elbow	E*d*	E*i* E*j* E*k* E*l*
Shoulder	I*f* I*i*	C*k* C*l* E*m*

These lower borders of the upper limb area of representation correspond absolutely closely to the levels given in the paper in 'Philosophical Transactions,' 1887.

In addition, however, we observed, to our surprise, that we occasionally obtained from the cortex of the foot of the ascending parietal gyrus movements of the upper limb, and not merely of the lowest segments, but also of the shoulder. Of fifteen experiments we noted at C*k* that the thumb was flexed twice, the fingers flexed twice in the interosseal position, and the shoulder adducted once at C*l*. The great rarity of this representation of the shoulder so low down on the outer or convex surface of the hemisphere, shows that it is quite exceptional, and no explanation of its occurrence in the evolution of the function of this part presents itself to us.

TABLE I.—Giving Absolute Number of Movements noted at any given Square, arranged in Order according to Frequency of Occurrence and not according to their Relative Sequence. See Table II. of "Marches."

Abbreviations to Table I.

T. = tongue.
M. = mouth.
M. ∠ = angle of mouth.
U.L. = upper lip.
Hd. = head.
F. = fingers.
Th. = thumb.
Sh. = shoulder.
W. = wrist.
Elb. = elbow.
S.P. = soft palate.
retr. = retraction.
∠ = angle of mouth.
opp. = opposite.
str. = straight.
protr. = protrude.
add. = adduct.
elev. = elevate.
inteross. = interosseal.
mastic. = mastication.
adv. = advance.
dors. = dorsum.
abd. = abduct.
flat. = flatten.
pout. = pouting.
bilat. = bilateral.
flex. = flexion.
ext. = extension.
sup. = supinate.
pron. = pronate.
rot. = rotate.

Square.						Number of observations.	Nil.
A.*b*.	Mastic., 4.	T. protr. str., 4.	M. open, 3.			15	10
A *c*	Mastic., 3.	T. protr. str., 3.	M. open, 2.			15	11
A.*d*.	Mastic., 4.	T. protr. str., 3. M. open, 3.		M. open, jaw to same side, 1. M. open, jaw to opp. side, 1. S.P. elevated bilaterally, 1.	Pouting bilat., 1. Grinding teeth, 1. Swallowing, 1.	15	5
A.*e*.	M. open, 6.	T. protr. str., 6.	Mastic., 5.	M. open, jaw to same side, 2.	M. open, jaw to opp. side, 1. S.P. elevated bilat., 1. Teeth grind from opp. to same side, 1.	15	4
A.*f*.	M. open, 9.	T. protr. str., 3. T. protr. to same side, 3.	Mastic., 3.	M. open, jaw to same side, 2. M. ∠, same side retract., 2.	M. ∠, same side elev., 1. Grind teeth, 1. Lips invert. (espec. opp. side), 1.	15	4
A.*g*.	M. open, 9.	T. protr. str., 3.	Mastic., 2.	M. ∠, same side retr., 1. Lips invert., 1.		15	4
A.*h*.	M. open, 6.	T. rolled to same side, dors. to cheek, 2.		T. protr. str., 1.		15	9
A.*i*.	M. open, 3.	T. protr. tip to opp. side, 2.		M. ∠, same side retr., 1.		15	10

TABLE I. (continued).

Square.							Number of observations.	Nil.
B.*b*.	M. open, 2.	Mastic., 1. T. protr. str., 1. T. protr. tip to opp. side, 1. Pouting, 1.					15	13
B.*c*.	Mastic., 5.	Pouting, 2.		M. open, jaw to same side, 1. M. open, 1. T. protr. str., 1. T. tip to opp. side, 1.			15	8
B.*d*.	Mastic., 7.	M. open str., 3.	M. open, jaw to same side, 2.		T. protr. str., 1. T. protr. tip to opp. side, 1. S.P. elev. bilat., 1. S.P. elev. opp. side, 1.	Cheek flattened, 1. Pouting, 1.	15	4
B.*e*.	Mastic., 8.	M. open str., 6.	T. protr. str., 5.	T. tip to opp. side, 2.	M. open, jaw same side, 1. M. ∠ adv., 1.		15	3
B.*f*.	M. open str., 9.	T. protr. str., 6.	Mastic., 4.	M. ∠ (same) retract., 2.	M. open, jaw same side, 1. T. rolled dors. to same cheek, 1. Cheek flattened, 1.	Pouting, 1. Lips inverted, 1.	15	4
B.*g*.	M. open str., 7.	T. dors. rolled to same cheek, 5.	M. open, jaw to same side, 4.	Mastic., 3.	T. tip to opp. side, 2. T. protr. str., 2. T. retracted, 2. M. ∠ opp. retr., 2. M. ∠ same retr., 2. Cheek flattened, 2.	Lips inverted, 1.	15	2

TABLE I. (continued).

Square.								Number of observations.	Nil.
B.*h*.	M. open str., 6.	T. retr., 3.	T. rolled, dors. to same cheek, 2.	T. protr. tip to opp. side, 1. M. open, jaw to same side, 1. M. ∠ opp. retract., 1. Lips invert., 1.				15	5
B *i*.	M. open str., 7.	T. protr. opp. side, 3.	T. retr., 2.	M. ∠ opp. retr., 2.	M. ∠, same retr., 1. Lips invert., 1.			15	6
B.*j*.	M. open str., 3.	M. opp. ∠ retr., 2.	M. same ∠ retr., 1. Lips invert., 1.	U.L. opp. elev., 1. Hd. turn, 1.				15	7
B.*k*.	M. opp. ∠ retr., 1.	Lips invert., 1.	U.L. opp. elev., 1.					15	10
C.*b*.	M. open, jaw to same side, 1.		Mastic., 1.	T. protr. str., 1.	T. dors. rolled to same cheek, 1.	M. ∠ same side retr., 1.	Pouting, 1.	15	12
C.*c*.	Mastic., 3.	M. open str., 3.	T. protr., 2.	T. retr., 1.	Pouting, 1.			15	9
C.*d*.	Mastic., 6.	T. protr. str., 5.	M. open str., 4.	M. open, jaw same side, 2.	S.P. elev. bilat., 1.			15	5
C.*e*.	M. open str., 7.	T. protr. str., 6.	Mastic., 5.	T. retr., 3.	T. dors. rolled to same cheek, 2. Pouting, 2.	Swallowing, 1.		15	5
C.*f*.	M. open str., 6.	Mastic., 4.	T. protr. str., 3.	Cheek flattened, 3.	M. open, jaw to same side, 1. T. protr. tip to opp. side, 1. T. dors. to same cheek, 1. U.L. opp. elev., 1.	Swallowing, 1. M. opp. ∠ retr., 1. Puckering, advancing both ∠ mouth, 1.		15	5

TABLE I. (continued).

Square.							Number of observations.	Nil.
C.*g*.	M. open str., 8.	T. dors. to same cheek, 2.	M. open, jaw to same side, 3.	Mastic., 2. T. protr. str., 2.	T. protr. to opp. side, 1. M. both ∠ retr., 1. M. opp. ∠ retr., 1.	Cheek flattened, 1. U.L. same side elev., 1.	15	3
C.*h*	M. open str., 7.	T. dors. to same cheek, 4.	Mastic., 3.	Cheek same side adv., 2.	M. open, jaw to same side, 1. T. protr. to opp. side, 1. T. retr., 1. M. both ∠ retr., 1. M. opp. ∠ retr., 1.	M. opp. elev., 1. Chin elev. bilat., 1. Chin opp. side elev., 1. Pouting, 1.	15	2
C.*i*.	M. open str., 8.	M. opp. ∠ retr., 3.	M. both ∠ retr., 2.	T. protr. to opp. side, 2.	T. protr. str., 1. T. dors. to same cheek, 1. M. both ∠ elev., 1.	M. opp. ∠ elev., 1. Chin opp. elev., 1. Mastic., 1.	15	5
C.*j*.	M. open str., 5.	M. opp. ∠ retr., 5.	M. both ∠ retr., 3.	T. protr. to opp. side, 2.	T. protr. str., 2.	Mastic., 1. T. dors. to same cheek, 1. T. retr., 1. F. inteross. flex., 1. Th. flexed, 1. M. same ∠ elev., 1. M. opp. ∠ elev., 1. Chin opp. side elev., 1. Hd. retr., 1.	15	6
C.*k*.	M. open str., 4.	M. both ∠ retr., 3.	M. opp. ∠ retr., 3.	T. protr. to opp. side, 2. F. inteross. flex., 2. Th. flexed, 2.	T. protr. str., 1. M. opp. ∠ elev., 1. Sh. add., 1.	Hd. retr., 1. Hd. to opp. side, 1.	15	6
C.*l*.	Hd. to opp. side, 3.	Sh. add., 1.	M. open, 1.					

TABLE I. (continued).

Square.							Number of observations.	Nil.
D.*c.*	M. open str., 2. Mastic., 2.	T. protr. str., 1. M. both ∠ retr., 1.	W. flex., 1. F. inteross. flex., 1.				15	11
D.*d.*	Mastic., 4.	M. open str., 3. T. protr. str., 3.	M. open, jaw to same side, 1. T. protr. to opp. side, 1.	M. both angles adv., 1. F. inteross. flex., 1.	Th. flex., 1.		15	9
D.*e.*	M. open str., 4.	Mastic., 3. T. protr. str., 3.	T. protr. to opp. side, 1. T. drawn to same cheek, 1.	T. retr., 1. M. opp. ∠ elev., 1.	M. both ∠ adv., 1. F. inteross. flex., 1.	Th. flex., 1.	15	7
D.*f.*	M. open str., 6.	T. protr. to opp. side, 4. M. opp. ∠ retr., 4.	Mastic., 3. T. dors. to same cheek, 3.	M. open, jaw to same side, 1. M. protr. str., 1.	Swallowing, 1. M. same ∠ retr., 1.	Pouting, 1. Both cheeks adv., 1.	15	3
D.*g.*	M. open str., 10.	M. open, jaw to same side, 4.	T. dors. to same cheek, 3. Same cheek puckered, 3.	Mastic., 2. T. protr. to opp. side, 2. T. protr. str., 2.	M. both ∠ retr., 1. M. opp. ∠ retr., 1.	M. both ∠ adv., 1. Opp. chin. elev., 1.	15	1
D.*h.*	M. open str., 6.	T. dors. to same cheek, 4.	Same cheek puckered, 3.	M. open, jaw to same side, 2. M. opp. ∠ retr., 2. M. both angles adv., 2.	Mastic., 1. M. closes, 1. T. protr. to opp. side, 1. Hd. retr., 1.	T. retr., 1. Opp. chin elev., 1. Pouting same side, 1. M. opp. ∠ adv., 1. M. same ∠ adv., 1.	15	4

TABLE I. (continued).

Square.							Number of observations.	Nil.
D.*i*.	M. opp. ∠ retr., 5.	M. open str., 2. T. protr. to opp. side, 2. M. opp. ∠ elev., 2. Opp. chin elev., 2.	Pouting, 2.	M. both ∠ retr., 1. M. same ∠ elev., 1. Lips inverted, 1 Hd. retr., 1.			15	4
D.*j*.	M. opp. ∠ retr., 12.	Pouting opp. side, 3.	T. protr. to opp. side, 2. M. opp. ∠ elev., 2.	Chin opp. side elev., 1. Hd. to opp. side elev., 1.	M. open str., 1. M both ∠ retr., 1.	T. retr., 1.	15	1
D.*k*.	M. opp. ∠ retr., 6.	M. opp. ∠ elev., 4.	T. protr. to opp. side, 2.	M. open, 1. M. both ∠ retr., 1.	Opp. chin elev., 1. Invert. lips, 1.	M. both ∠ adv., 1. Hd. to opp. side, 1.	15	5
D.*l*.	Hd. to opp. side, 4.	M. opp. ∠ retr., 3.	M. both ∠ retr., 1.	M. opp. ∠ elev., 1.	F. ext., 1.		15	7
D.*m*.	Hd. to opp. side, 4.						15	11
E.*c*.	M. pouting opp. side, 2.		M. opp. side rolled in, 1.				15	12
E.*d*.	Mastic., 1. Elb. flexed, 1.	M. opp. ∠ retr., 1. Wrist, 1.	M. opp. ∠ elev., 1. Fingers, 1.	M. opp. ∠ pursed, 1. Th. ext., 1.	M. opp. side rolled in, 1.	Cheek of same side flattened, 1.	15	9
E.*e*.	M. opp. side rolled in, 3.		M. opp. ∠ retr., 2. Th. abd. and flex., 2.	M. both ∠ elev., 1. M. opp. ∠ elev., 1.	M. opp. side pont., 1. M. opp. side purs., 1.		15	5
E.*f*.	Mastic., 2. T. dors. to same side, 2.		M. both ∠ retr., 2. M. opp. ∠ retr., 2.	M. bilat. pout., 2.	M. open, 1. M. opp. ∠ elev., 1.	Cheek same side flat, 1. Th. add., 1.	15	5

TABLE I. (continued).

Square.							Number of observations.	Nil.
E.*g*.	M. opp. ∠ retr., 7.	M. open, 4.	M. opp. ∠ elev., 3. T. tip to opp. side, 3.	Mastic., 2. M. both ∠ retr., 2. M. pursing, 2.	M. open, jaw to same side, 1. T. dors. to same side, 1. M. ∠ same side retr., 1.	Cheek of same side elev., 1. M. bilat. pout., 1. Cheek of same side flat, 1. Th. add., 1.	15	1
E.*h*.	M. opp. ∠ retr., 3.	M. open str., 2. M. open jaw to same side, 2. Lips same side rolled in, 2.	T. protr. tip to opp. side, 2. M. opp. ∠ elev., 2. Cheek same side flat, 2.	Mastic., 1. T. rolled over dors. to same side, 1. Chin bilat. elev., 1.	M. bilat. pout., 1. M. bilat. purs., 1. Lips bilat. rolled in, 1.	Cheeks bilat. flat., 1.	15	5
E.*i*.	M. opp. ∠ retr., 7.	M. opp. ∠ elev., 4.	M. open 2. T. protr. tip to opp. side, 2. Lips opp. side rolled in, 2.	T. protr. str., 1. T. dors. rolled to same side, 1.		Opp. chin elev., 1. Elb. flex., 1.	15	2
E.*j*.	M. opp. ∠ retr., 9.	M. opp. ∠ elev., 6.	M. open, jaw to same side, 2. T. protr. tip to opp. side, 2.	Chin opp. elev., 2. Hd. to opp. side, 2.	M. open str., 1. T. dors. rolled to same side, 1. Lips opp. side rolled in, 1.	Elb. flex., 1. W. ext. and pron., 1. Hd. retr., 1.	15	1
E.*k*.	M. opp. ∠ retr., 8.	M. opp. ∠ elev., 5.	M. open str., 2. T. protr. tip to opp. side, 2. Chin opp. side elev., 2.	Elb. flex., 2. F. flex., 2.	T. dors. rolled to same side, 1. Lips opp. side rolled in, 1. Th. flex., 1.	Opp. eyelids closed, 1. W. sup. and pron., 1. Hd. to opp. side, 1.	15	3

TABLE I. (continued).

Square.		Number of observations.	Nil.
E.*l*.	Elb. flex., 3. M. opp. ∠ elev., 2. M. opp. ∠ retr., 1. Opp. eyelids close, 1. Eyes to opp. side, 1. F. ext. 1. Chin opp. side elev., 1. W. sup., 1.	15	8
E.*m*.	Opp. cyelids close., 1. Sh., rot. in., 1. Fingers, 1. Hd. to opp. side, 1.	15	12
F.*d*.	M. opp. ∠ elev., 1. M. opp. side pout., 1. F. ext., 1. Th. ext., 1.	15	11
F.*e*.	M. opp. ∠ retr., 4. Opp. lower lip depress., 2. Mastic., 1. M. bilat. purs., 1. Th. opp., 1. Opp. lips roll in, 2. M. bilat. pout., 1. F. add., 1. Th. flex., 1. Th. ext., 2.	15	4
F.*f*.	M. opp. ∠ retr., 4. M. opp. ∠ elev., 3. M. bilat. pout., 2. Th. opp., 1. F. ext., 1. Mastic., 1. Opp. lower lip depress., 1. Opp. lips roll, in 1 Th. ext., 2. Elb. flex., 1. W. ext., 1. M. both angles retr., 1. M. bilat. purs., 1.	15	4
F.*g*.	M. opp. ∠ retr., 6. M. opp. ∠ elev., 5. Opp. lower lip depress., 3. M. bilat. purs., 2. T. protr. tip to opp. side, 1. M. bilat. pout., 1. Th. ext., 1. Bilat. drawing forward of lips, 3. T. dors. to same side, 1. F. ext., 1.	15	0
F.*h*.	M. opp. ∠ retr., 4. M. bilat. pout., 3. M. open str., 2. Mastic., 1. M. same ∠ elev., 1. Opp. chin elev., 1. Hd. retr., 1. M. opp. ∠ elev., 4. T. dors. to same side, 2. T. protr. tip to opp. side, 1. Opp. lower lip depress., 1. M. bilat. purs., 1.	15	4
F.*i*.	M. opp. ∠ retr., 7. Opp. eyelids closed, 4. M. opp. ∠ elev., 3. Elb. flex., 1. Hd. retr., 1. T. protr. tip to opp. side, 1. T. protr. str., 1.	15	2

TABLE I. (continued).

Square.								Number of observations.	Nil.
F.*j*.	M. opp. ∠ retr., 7.	Opp. eyelids closed, 5.	M. opp. ∠ elev., 4.	Eyelids bilat., blink, 3.	Elb. flex., 2.	Opp. lower lip roll in, 2.	Hd. to opp. side, 1.	15	0
F.*k*.	M. opp. ∠ elev., 4.	M. opp. ∠ retr., 4. Opp. eyelids close, 3.	Elbow, 2. Hd. to opp. side, 2.	Hd. retr., 1.	Opp. chin, elev., 1. M. purs., 1.	Opp. lower lip roll in, 1.		15	6
F.*l*.	Opp. eyelids close, 3.	M. opp. ∠ elev., 2. Hd. to opp. side, 2.	M. opp. ∠ retr., 1.					15	5
F.*m*.	M. opp. ∠ retr., 2. Hd. to opp. side, 2.	Opp. eyelids close, 1. Eyes to opp. side, 1.	F. inteross. flex., 1.					15	12
G.*d*.	F. opp., 2. Th. opp., 2.	M. opp. ∠ retr., 1. M. opp. ∠ elev., 1.	Opp. lower lip depress., 1.					15	13
G.*e*.	F. ext., 4. Th. ext., 4.	M. opp. ∠ elev., 2.	M. opp. ∠ retr., 1. Opp. lips roll in, 1.	M. bilat. purs., 1. Opp. lower lip depress., 1.	M. opp. ∠ adv., 1.	W. sup., 1. W. ext., 1.		15	9
G.*f*.	M. opp. ∠ elev., 6.	M. opp. ∠ retr., 5.	M. ∠ bilat. adv., 2. Th. ext., 2.	M. bilat. pout., 1. M. bilat. purs., 1.	Lower lip depress., 1. W. flex., 1.	Th. flex., 1.		15	3
G.*g*.	M. opp. ∠ elev., 7. M. opp. ∠ retr., 7.	M. opp. ∠ adv., 3. M. opens, 3.	M. bilat. pout., 2. Opp. lower lip depress., 2.	T. same side retr., 1. Cheek on same side puckered, 1.	W. ext., 1. Th. ext., 1.	F. ext., 1.		15	0

TABLE I. (continued).

Square.								Number of observations.	Nil.
G.*h*.	M. opp. ∠ elev., 7.	M. opp. ∠ retr., 4.	M. opens, 2. T. protr. tip to opp. side, 2.	Th. ext., 2. Opp. cheek puckered, 2.	T. retr., 1. M. same ∠ retr., 1. M. opp. ∠ adv., 1.	M. bilat. pout., 1. M. ∠ bilat. adv., 1. W. ext., 1.	F. ext., 1.	15	2
G.*i*.	M. opp. ∠ elev., 6.	Opp. eyelids close, 4.	M. opp. ∠ retr., 3.	Opp. lips roll in, 2.	W. pron., 1.			15	4
G.*j*.	Opp. eyelids close, 5.	M. opp. ∠ retr., 4.	M. opp. ∠ elev., 3.	Opp. lower lip roll in, 2.	T. protr. tip opp. side, 1. Eyelids bilat. closed, 1.	F. ext., 1. Th. ext., 1.		15	5
G.*k*.	M. opp. ∠ retr., 3.	Opp. lips roll in, 2. Hd. to opp. side, 2.	Opp. eyelids close, 1.	Elb. flex., 1. F. ext., 1.				15	8
G.*l*.	M. ∠ retr., 3.	Eyes to opp. side, 2.	Opp. lower lip roll in, 1.	W. sup., 1.	F. ext., 1.	Hd. to opp. side, 1.		15	11
H.*e*.	M. opp. ∠ retr., 3.	M. bilat. purs., 1.	Opp. lips roll in, 1.					15	11
H.*f*.	M. opp. ∠ retr., 6.	M. opp. ∠ elev., 4. Th. flex., 4.	M. bilat. purs., 2. F. flex., 2.	Opp. lips roll in, 1. M. opp. ∠ adv., 1.	Elb. flex., 1. W. sup., 1.	W. ext., 1. Th. add., 1.		15	4
H.*g*.	M. opp. ∠ retr., 9.	M. opp. ∠ elev., 5.	Th. flex., 3.	Opp. lower lip depress, 2. F. flex., 2.	M. open, 1. M. bilat. purs., 1.	M. opp. ∠ adv., 1. Opp. eyelids closed, 1.	Elb. flex., 1. W. sup., 1.	15	3

TABLE I. (continued).

Square.							Number of observations.	Nil.
H.*h*.	M. opp. ∠ retr., 8.	M. opp. ∠ elev., 6. Th. flex., 6.	Index finger ext., 3.	Opp. eyelids close, 1.	Elb. flex., 1.		15	0
H.*j*.	Opp. eyelids close, 6.	M. opp. ∠ retr., 5.	M. opp. ∠ elev., 3.	Th. flex., 2.	Opp. lips roll in, 1.	F. flex., 1.	15	5
H.*k*.	M. opp. ∠ retr., 1.	M. opp. ∠ elev., 1.	Opp. lips roll in, 1.	Opp. eyelids close, 1.			15	12
H.*l*.	M. opp. ∠ retr., 2.	M. open, 1.	Opp. lips roll in, 1.				15	13
H.*m*.	Hd. to opp. side, 1.						15	14
I.*e*.	M. opp. ∠ retr., 4.	Eyes open, 1	Elbow flex., 1.	W. sup., 1.	Fingers, 1.	Hd. to opp. side, 1.	15	11
I.*f*.	M. opp. ∠ retr., 3. M. opp. ∠ elev., 3.	Opp. lower lip depress., 2. Thumb, 2.		Hd. to opp. side, 2.	Opp. lips roll in, 1. Opp. eyelids close, 1.	Fingers, 1.	15	7
I.*g*.	M. opp. ∠ elev., 6.	Fingers, 5. Thumb, 5.	Opp. eyelids close, 4.	M. opp. ∠ retr., 4.	Opp. lower lip depress., 3.	M. opp. pursed, 1. Hd. retract., 1. Hd. to opp. side, 1.	15	3
I.*h*.	Thumb, 6.	M. opp. ∠ elev., 4. Fingers, 4.	M. opp. ∠ retr., 3.	Opp. lower lip depress., 2. Opp. eyelids close, 2.	Hd. to opp. side, 1.		15	6
I.*i*.	Thumb, 6.	Opp. eyelids close, 3.	M. opp. ∠ retr., 1.	M. opp. ∠ elev., 1.	Opp. lip depress., 1. Elbow, 1.	Sh. 1. Fingers, 1. Wrist, 1.	15	8

TABLE I. (continued).

Square.		Number of obser-vations.	Nil.
J.*f*.	Thumb, 3. M. opp. ∠ retr., 2. M. opp. ∠ elev., 1. Opp. eyelids close, 1. Wrist, 3. Fingers, 3. Shoulder, 3. Opp. lower lip depress., 1. Hd. to opp. side, 1.	15	9
J.*g*.	M. opp. ∠ retr. 2. M. opp. ∠ elev., 1. Opp. lower lip depress., 1. Wrist flex., 1.	15	13
J.*h*.	M. opp. ∠ retract, 1. M. opp. ∠ elev., 1. Hd. to opp. side, 1.	15	12
J.*i*.	Opp. eyelids closed, 1. (Face only observed).	15	14
J.*j*.			
K.*f*.			
K.*g*.			
K.*h*.			
K.*i*.			

MARCHES.

Under this heading we wish to describe, in the meaning of the word as originally used by Dr. HUGHLINGS JACKSON, such sequences by movements as we occasionally observed to take place.

At the outset we would state that a great difference characterises the area of representation for the face as contrasted with that for the limbs. Whereas it was possible in the case of the limbs to make out a definite march for individual parts of the cortex, we have not been able to find sufficient examples of such similarity as to justify us in attributing a definite march to the different parts of the area of representation for the face, but although this exact localisation is not possible the representation of the primary movement, as given in the accompanying list, is such as we have already described in each case.

We have therefore simply appended a list of the sequences of movements or marches arranged in the order in which they most frequently occurred.

TABLE II.

Marches.		Number of squares at which observed.
Primary	Mouth opens	7
Secondary	Mastication movements, tongue protruded	
Primary	Bilateral pouting	5
Secondary	Mouth opens, jaw to same side	
Tertiary	Mastication movements	
Primary	Opposite angle retracted or elevated	5
Secondary	Tongue protruded, tip to opposite side	
Primary	Both angles bilaterally retracted	4
Secondary	Mouth opens, tongue tip to opposite side	
Primary	Mouth retracted to opposite side, opposite lower lip inverted	4
Secondary	Opposite eyelids closed	
Primary	Mouth opens	3
Secondary	Tongue protruded, tip to opposite side	
Primary	Mouth opens	3
Secondary	Masticatory movements, tongue protruded to opposite side, and retracted	
Primary	Pouting or pursing of lips	3
Secondary	Opposite angle retracted	
Tertiary	Tongue rolled to same side	
Primary	Pouting or pursing	3
Secondary	Opposite angle retracted or elevated	
Tertiary	Elevation of opposite lower lip	
Primary	Angle of mouth retracted on same side	2
Secondary	Mouth opens with retraction of opposite angle	
Tertiary	Mastication with protrusion of tongue	
Primary	Mouth opens straight	2
Secondary	Tongue advanced	
Tertiary	Both angles of mouth retracted	
Primary	Mouth opens wide	2
Secondary	Tongue retracted concave to opposite side, dorsum to same cheek	
Primary	Opposite lower lip rolled in	2
Secondary	Opposite upper lip rolled in	
Tertiary	Opposite angle of mouth retracted	
Primary	Pouting and pursing, especially of opposite side	2
Secondary	Opposite lower lip everted and depressed	
Tertiary	Opposite angle of mouth retracted	
Primary	Mouth opens	1
Secondary	Tongue protruded to same side	
Primary	Mouth pursed up	1
Secondary	Mouth opened	
Tertiary	Tongue rolled over to same side	
Primary	Pursing of mouth	1
Secondary	Closed mouth drawn to opposite side	
Primary	Opposite eyelids closed, opposite side of mouth retracted	1
Secondary	Opposite lower lip inverted	

FIG. 1

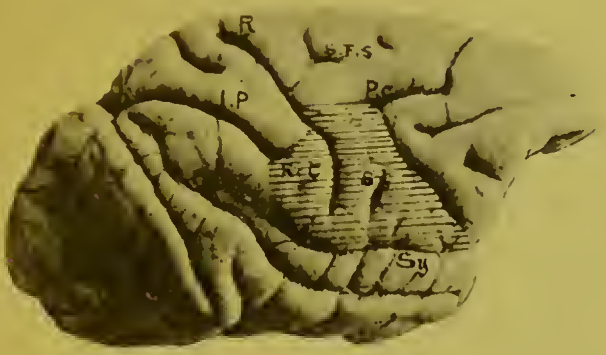

FIG. 2.

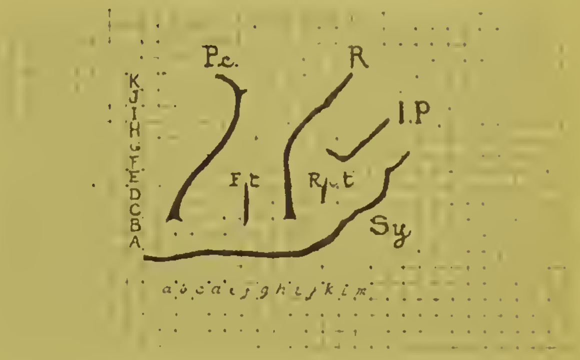

FIG. 3.

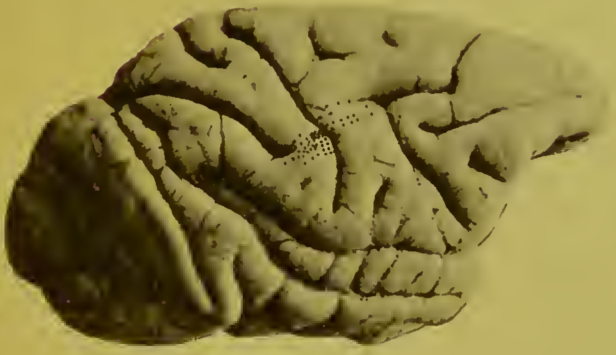

FIG. 4.

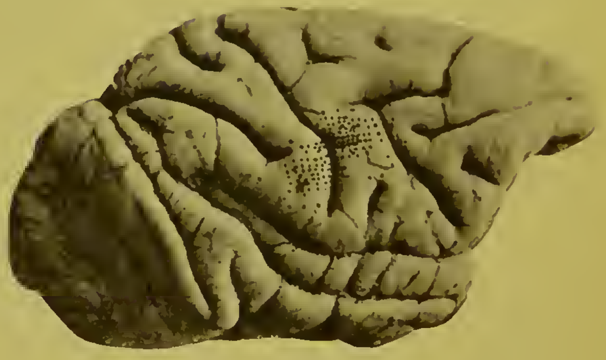

FIG. 5.

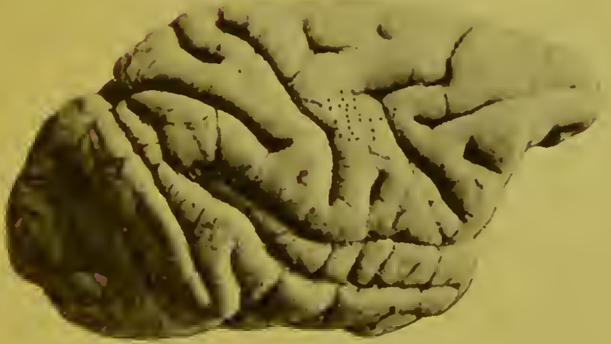

FIG. 6.

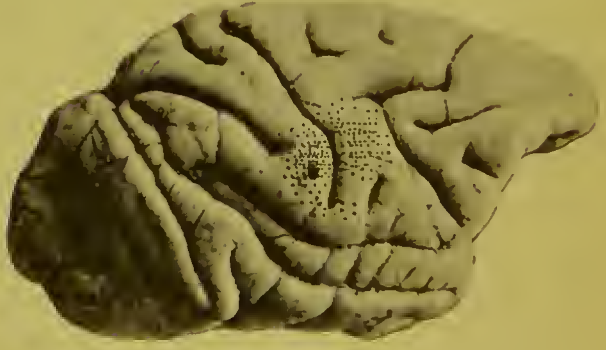

FIG. 7.

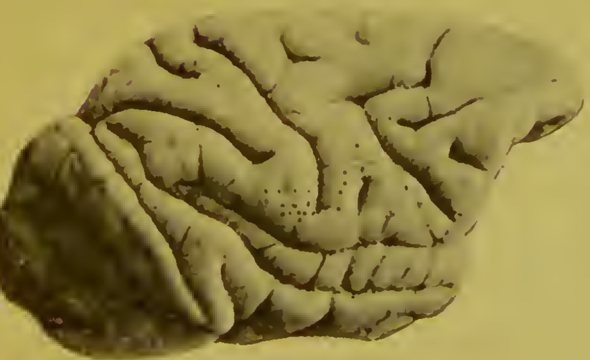

FIG. 8.

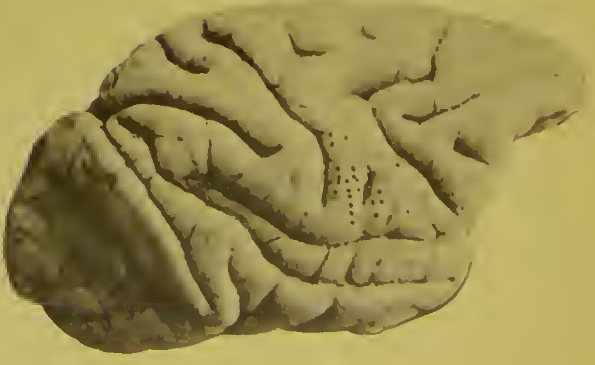

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FIG. 9.

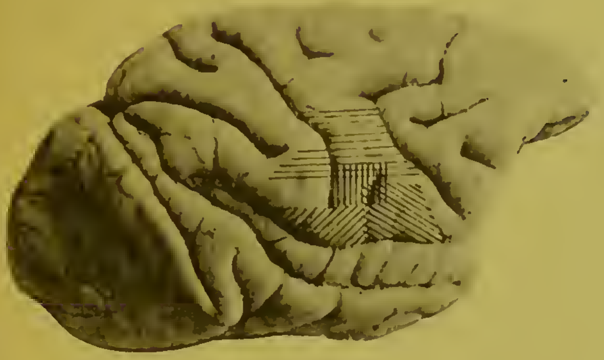


FIG. 10.

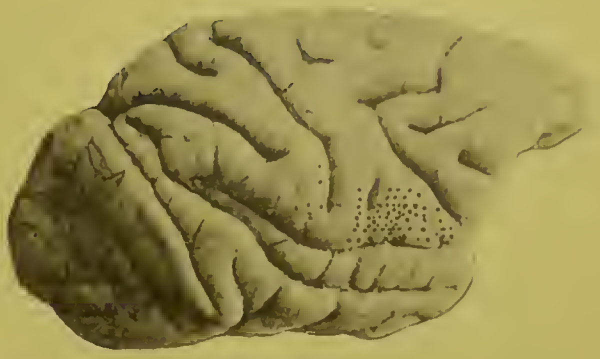


FIG. 11.

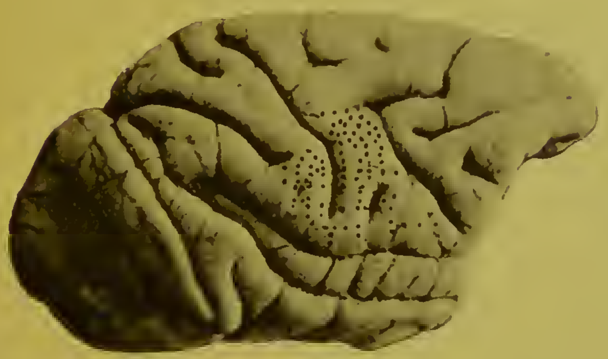


FIG. 12.

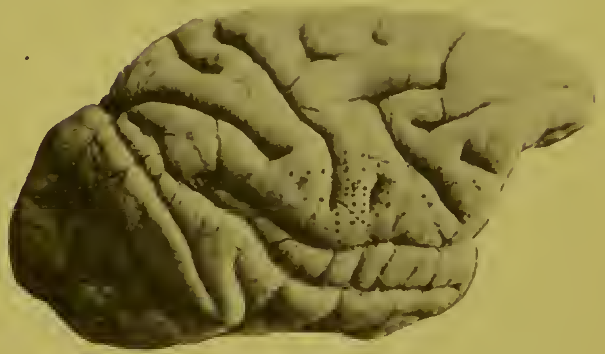


FIG. 13.

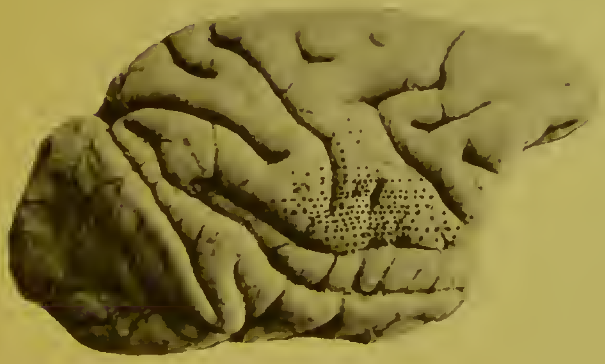


FIG. 14.

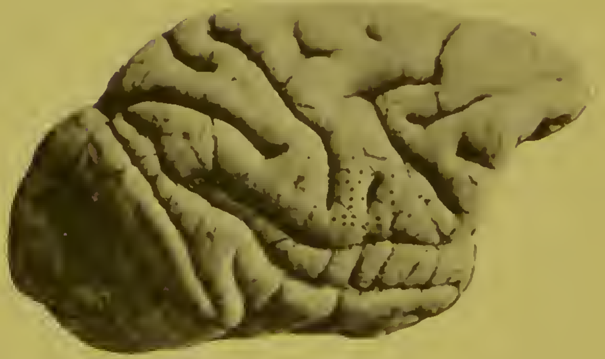


FIG. 15.

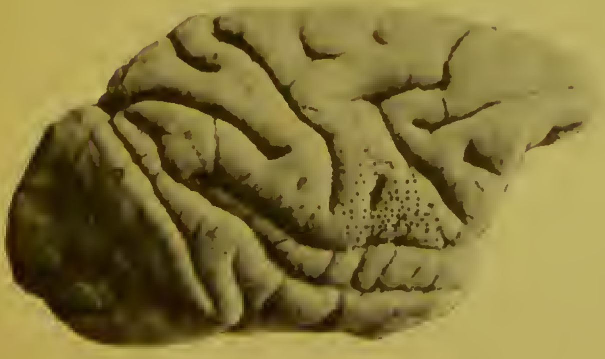
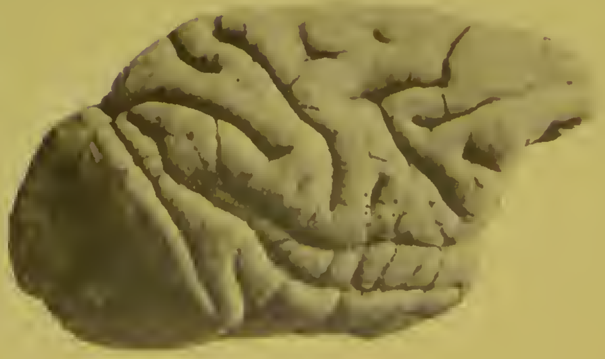


FIG. 16.



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VIII. *An Experimental Investigation of the Central Motor Innervation of the Larynx.*

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(*From the Laboratory of the Brown Institution.*)

Received June 17,—Read June 19, 1890.

[Plates 31, 32.]

Part I.—Excitation-experiments.

a. *Introduction.*

In the course of observations dealing with the physiology of the motor innervation of the larynx, the results of which were embodied in a paper recently presented by one of us (F. S.) to the Royal Society,* it was shown that the central innervation of the larynx played a much more important *rôle* in the function of respiration than had previously been accorded to it. More especially it was shown that certain nerve-centres were constantly at work in maintaining a reflex-tonus of the abductor muscles (posterior crico-arytænoids) indispensable for the mechanism of quiet respiration in Man.

In 1880, 1881 and 1883† it had been shown by one of us (F. S.) that these same muscles (the abductors) were more liable to degenerative changes in cases of organic disease of the motor nerves of the larynx from the medulla oblongata downwards, and at the same time that functional disorders of the laryngeal motor apparatus almost exclusively affected their antagonists, the adductors. The explanation of all these different phenomena presented great difficulties, and, although light was thrown upon them in very various and unlooked-for ways, it soon became evident that neither clinical and pathological observations in Man alone, nor experiments upon the peripheral nerve-mechanism of animals, would suffice to solve all the questions here involved.

Now, the fact just mentioned—viz., that in functional disorders (*e.g.*, hysterical aphonia) those motor laryngeal nerve-fibres only which subserve the volitionary function of the larynx (*i.e.*, phonation) ordinarily suffer, whilst, on the other hand, in organic disease those fibres are usually primarily affected which are engaged in maintaining the automatic process of laryngeal respiration—seemed to indicate that there must be a central differentiation corresponding to these varied phenomena. Hence it was that the idea of the present research occurred to us.

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* "On the Position of the Vocal Cords in Quiet Respiration in Man, and on the Reflex-tonus of their Abductor Muscles." 'Roy. Soc. Proc.,' 1890 (vol. 48, p. 403).

† (*a*) Foot note in German Edition of Morell Mackenzie's 'Diseases of the Throat and Nose,' vol. 1, p. 574.

(*b*) 'Archives of Laryngology,' July, 1881.

(*c*) 'Berliner Klinische Wochenschrift,' No. 46, *et seq.*, 1883.

In planning such an investigation we naturally turn first to the subject of the cortical representation of the larynx—a problem which, first touched upon by FERRIER and DURET, has been treated in detail by H. KRAUSE at the instigation of H. MUNK, and by MASINI.

From this point we might proceed to the consideration of the fibres leading from the cortex to the lower centres in the medulla, as they pass through the corona radiata and the internal capsule. The investigation of these fibres by means of the excitation-method has, so far as we know, not been undertaken by any previous observer, though some work by the ablation and degeneration method has been performed by KRAUSE. This latter method and its results will be fully dealt with by us in a subsequent paper.

Finally, we discuss the results of excitation of the central mechanism in the bulb, a branch of the subject which we commenced four years ago, and which also has not been treated, to our knowledge (confirmed by Professor GAD), by any previous observer.

Before passing to a complete historical retrospect of the question, and before describing the method of our own experiments, we may state that, since we have found certain important differences in the central structural arrangements in different species of animals, and also in animals of different ages belonging to the same species, it is essential that these should first be prominently and clearly expressed, in order that some discrepancies which exist in the statements of previous investigators and the classification of our own results might be properly understood.

To the same category belongs the question of the action of anæsthetics upon the neuro-muscular system, a question the importance of which for the present investigation can hardly be exaggerated ; since, for reasons which we will further discuss, the effect attained by exciting any given centre may be entirely modified by the mere degree of anæsthesia affecting the peripheral mechanism of nerve-endings and muscles.

In a previous communication* we have shown the importance of the action of ether upon the peripheral nervous system, a factor which must be properly discounted in considering the action of the anæsthetic upon the nervous mechanism as a whole.

These considerations of species, age, and anæsthesia will compel us to further subdivide the great groups into which we have arranged our facts.

In the following historical retrospect of the results obtained by previous investigators we have thought it best (to avoid misconception) to place each writer in the chronological order of the appearance of his publication.

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* "On an apparently peripheral and differential action of Ether upon the laryngeal muscles," 'British Medical Journal,' 1886.

b. *Historical Retrospect.*

Although various authors have observed the changes in thoracic respiration following excitation of the central nervous system, but few have studied the relationship of the latter to the larynx, either so far as respiration or as phonation is concerned.

As this relationship is the immediate subject of this paper, we shall confine ourselves in this retrospect to a brief *résumé* of the results of those authors who have directly investigated, either experimentally or clinically, the question here at issue.

On the experimental side undoubtedly **Ferrier**[*] was the first worker in the field of excitation. In the first edition of his well-known work he describes an instance in which excitation of a certain cortical area in the Dog elicited barking, and observes that similar observations had been made by him repeatedly.

Shortly afterwards **Duret**,[†] of Paris, referred to the same subject in connection with his cortical ablation and compression experiments, and reported similar results.

Although subsequent experimentation has shown that both these observers did not accurately localise the *focus* of the representation of phonation in the cortex, to them, undoubtedly, belongs the priority of the idea of a special representation of this function in the cortex.

Seven years after **Ferrier's** reference to the question the subject was, at the suggestion of H. **Munk**, specially studied by H. **Krause**,[‡] who was the first to localise accurately the phonatory area in the cortex of the Dog's brain. He made six excitation-experiments on Dogs, from which he localised the movement of closure of the glottis (always bilateral adduction) to be represented in the isthmus ("STIEL") of the præfrontal (præcrucial) gyrus. To his ablation and degeneration experiments we shall make reference in a future communication.

In his great work on the functions of the brain, **François Franck**[§] states that excitation of the "zone motrice" of the cortex produces changes in the thoracic respiratory movements according to the duration and intensity of the excitation. These changes are acceleration, slowing, and variations of amplitude. He does not consider that respiratory centres can be considered to exist in the cortex cerebri, or that there is any differential representation of the larynx or other parts of the respiratory apparatus.

In the epileptic convulsion evoked by cortical excitation he observed what we have confirmed and extended, viz., that in the tonic stage the glottis is shut, whereas in the clonic stage the cords execute movements synchronous with the twitchings of the thoracico-abdominal respiratory muscles.

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[*] 'Functions of the Brain.'

[†] 'Traumatismes cérébraux,' 1878, p. 142.

[‡] "Ueber die Beziehungen der Grosshirnrinde zu Kehlkopf und Rachen," 'Archiv für Anatomie und Physiologie, Physiol. Abth.,' 1884. This was preceded by a note under the same title, in the 'Sitzungsberichte der Kgl. Preuss. Akademie der Wissenschaften zu Berlin,' November, 1883.

[§] François Franck, 'Leçons sur les Fonctions Motrices du Cerveau,' Paris, 1887, pp. 146–8.

Masini[*] made in 1888 a series of both excitation and ablation experiments on the cortex of Dogs. In the former he found in four cases that excitation with weak currents produced earlier movements of the opposite vocal cord, followed by later and slower movements of the cord corresponding to the side of stimulation. He is the only experimenter, so far as we know, who has obtained such unilateral results. With stronger currents he obtained bilateral movements. According to his views the representation of the adductory movements of the vocal cords is spread over the whole motor area, though focussed in the centres for the soft palate and tongue.

Aronsohn[†] mentions in a paper, published in the same year, briefly, that in his experiments he could not obtain any definite reply to the question whether the adductory movements of the vocal cords observed by him were actually due to the stimulation of the brain.

Mott,[‡] in repeating our observations, corroborated our results.

Two very important papers on the root-fibres of the motor nerves of the larynx, by Grossmann[§] and Grabower[||] respectively, we only desire in this connection to mention by title, as the subject of their researches rather refers to the peripheral part of the nervous mechanism of the larynx.

The above short list comprises, so far as we know, all experimental contributions to this question, in which the intrinsic laryngeal movements have been actually observed or recorded, when the central nervous system has been stimulated.

The clinical evidence concerning the relationship of the larynx to the higher nervous centres is also very limited.

That lesions of the medulla oblongata may and do occasionally cause laryngeal paralysis, is, of course, admitted on all hands. In such cases it is, correctly speaking, rather a lesion of the vago-accessory nucleus and fibres in the medulla oblongata than a genuine central affection, to which the laryngeal paralysis must be attributed.

With regard to the higher nervous centres, however (cortex and internal capsule), matters are very different.

Although a certain number of cases have been published (*e.g.*, by Andral, Gerhardt, Friedreich, Foville, Duval, Löri, Lewin, Livio Ronci, Luys, Cartaz, Massei, &c.[¶]), in which simultaneously with organic lesions of the higher centres vocal disturbances or even laryngeal paralyses have been observed, no conclusions can be drawn from them for the decision of the present question, because all of them are in some way or other incomplete. In some of them the diagnosis of a cerebral lesion is not at all beyond doubt, in others multiple lesions existed, in a third category no laryngoscopic examination had been made, and again in others either no autopsy had taken place, or the descriptions of the latter, when made, are defective with regard to the condition of the medulla oblongata, the peripheral parts of the laryngeal nerves, the microscopic examination of the medulla, the nerve fibres, and the muscles themselves, &c.

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[*] 'Archivi Italiani di Laryngologia,' Napoli, April, 1888, p. 45.

[†] "Zur Pathologie der Glottiserweiterung," 'Deutsche Med. Wochenschr.,' 1888.

[‡] 'Brit. Med. Journal,' 1890.

[§] "Ueber die Athembewegungen der motorischen Kehlkopfnerven, II. Theil," 'Sitzungsberichte der Kais. Akad. d. Wissensch. zu Wien,' November, 1889.

[||] "Das Wurzelgebiet der motorischen Kehlkopfnerven," 'Centralblatt für Physiologie,' January 4, 1890.

[¶] The literature of these cases will be found in Masini's, Garel and Dor's, and in Rossbach's papers hereafter referred to in the text. They are not quoted here at length, because these authors themselves admit that they cannot claim to be of a decisive character for the question at issue.

In 1884 Bryson Delavan* called attention to the possibility which existed in his opinion, viz., of localising from clinical observation the cortical motor centre for the larynx. Of the two cases, however, upon which he based his views, in one (Seguin's) no laryngoscopic examination had been made, whilst he himself frankly stated some years afterwards,† that in the second one, his own, in which he had attributed the laryngeal paralysis to a cortical lesion, the post-mortem examination had established the fact that in reality it was of bulbar nature.

In 1886 Garel‡ recorded an observation, to which he added, in conjunction with M. Dor, another in 1890, which proved,§ in the opinion of these authors, that unilateral laryngeal paralysis could be caused by a unilateral lesion of the opposite hemisphere or internal capsule. We have elsewhere|| taken exception to the interpretation given by these authors to the paralysis observed in their cases, because (*a*) the medulla oblongata was not microscopically examined at the post-mortem examination, and (*b*) the *total* paralysis (respiratory as well as phonatory) of the vocal cord observed in their cases is according to our ablation-experiments absolutely incompatible with the idea of its being due to a *cerebral* lesion.

Recently Rossbach¶ has published a very interesting paper on the subject, in which from a carefully observed case under his own care he draws the conclusion that unilateral paralysis of a vocal cord may be caused by a lesion of the opposite insula. Seeing however, that in his case there was atrophy of the corresponding side of the tongue due to an undoubted lesion of the ganglionic cells of the hypoglossal nucleus in the medulla oblongata, and that the integrity of the vago-accessory nucleus in the medulla was merely *surmised* from the fact, that the fibres of the nerve itself, and of the laryngeal muscles, had undergone no atrophy, while it was not at all shown that the

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* 'Compte-rendu des Travaux de la Section de Laryngologie du VIII. Congrès International Périodique des Sciences Médicales.' Copenhague, 1884, p. 17.

† 'Transactions of the American Laryngological Association,' 1888, p. 195.

‡ 'Annales des Maladies de l'Oreille et du Larynx,' May, 1886.

§ *Ibidem*, April and May, 1890.

|| 'Annales des Maladies de l'Oreille et du Larynx,' May and June, 1890.

¶ "Localisation des corticalen Stimmcentrums beim Menschen." 'Deutsches Archiv für klinische Medicin,' vol. 46, March, 1890.

laryngeal paralysis had existed so long that atrophy ought necessarily have followed, we cannot admit this case as actually proving such a relationship as that claimed by the author.

Finally, at this moment a paper on the subject is in course of publication from the pen of SCHEFF,[*] the outcome of which cannot yet be foretold.

The general observations of LANNOIS[†] bring nothing new, whilst GOTTSTEIN[‡] considers the question of the existence of a cortical centre for the larynx in man as still open.

This short list practically exhausts the clinical material in connection with the subject.

c. *Methods of Experimentation.*

The different points to be considered under this heading may conveniently be grouped in the following manner :—

1. Electrical methods.
2. Operative technique.

1. *Electrical methods.*—The excitation either of the cortex, corona radiata, or bulb was furnished by the secondary coil of a DU BOIS-REYMOND inductorium of the ordinary pattern, the distances of the secondary coil being marked in millimetres from a zero point where the primary coil was completely covered. In the later experiments we always employed a special inductorium with the HELMHOLTZ side wire, very kindly graduated for one of us by Professor KRONECKER, according to the manner he has published elsewhere, and by means of which alone is obtained an accurate knowledge of the increase in the strength of the stimulus when the secondary coil is pushed towards and over the primary. To facilitate the various references to the strength of the current in this paper we now give in parallel columns the divisions in millimetres according to the old method, and opposite them the divisions according to KRONECKER'S method. The battery elements employed were either one Daniell cell, one 1 litre bichromate cell, (GRENET), or a thermoelectric element, 16 cm. high, 14 cm. diameter, of 19 metallic junctions.

DU BOIS-REYMOND inductorium. cm.	0.	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.	23.	24.	25
Divisions of current KRONECKER inductorium.	13,000	12,500	12,000	11,250	10,270	9,250	8,500	7,300	6,300	5,300	4,300	3,300	2,400	1,700	1,000	Fraction over 600	420	300	250	180	130	87	70	58	48	41

The electrodes employed were always fine platinum points which, in exciting the cortex, were fixed 2 mm. apart, but in exciting the corona radiata, internal capsule, or bulb were placed 1 mm. apart. The stimulus was kept applied to the cortex for different periods of time according to varying circumstances. Thus if a very minimal stimulus was being employed it was necessary, in order to judge of its effect upon the cortex, to prolong the excitation during several respiratory movements of the vocal cords, *i.e.*, from 5 to 10 seconds. If, however, the stimulus was markedly adequate so that an unmistakeable effect was produced immediately and ceased directly the stimulation was discontinued, then the application of the electrodes was only maintained for from 1 to 2 seconds, so as not to exhaust the cortex.

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[*] "Zur Pathologie d. Motilitätsstörungen d. Kehlkopfs." 'Allg. Wien. Med. Zeitung,' June, 1890.

[†] "Y a-t-il un Centre cortical du Larynx ?" 'Revue de Médecine et de Chirurgie,' August, 1885.

[‡] 'Die Krankheiten des Kehlkopfs,' Dritte Auflage, 1890, p. 344.

2. *Operative technique.*—The first point to be considered of course is the anæsthesia, the importance of which has been already alluded to, and is considered in further detail on p. 195. We may say at once that we have almost invariably used ether, in a few cases also in part chloroform ; but inasmuch as the latter did not show any specific effect, differing much from that of ether, it is sufficient only to allude to it here as it may chance to be mentioned hereafter. The narcotisation was always conducted in the following manner :—The ether was first given by inhalation, and then complete unconsciousness having been produced tracheotomy was next performed and the anæsthetisation continued through a funnel and short[*] piece of rubber tubing, the funnel resting on cotton wool wet with ether and covered with a cloth. This method had the advantage that as it was usually found far more convenient to inspect the larynx from below all trouble connected with the inhalation of the narcotic was avoided, and as the trachea was always completely divided it was readily moved aside without twisting the larynx to either side, and consequently an uninterrupted view obtained. Furthermore, if too much anæsthetic was given by mistake, it was easy to restore the animal by inflation.

The tracheotomy having been done, as large a cannula as possible was inserted and fitted as above stated.

The animal was secured in a prone position and the operation proceeded with to expose the central parts of the brain. These may be referred to as cortex, corona radiata, internal capsule, and bulb. The second and the third of course consist only of fibres, whereas in the first and last case additional complications arise and extra precautions have to be taken owing to their being central apparatuses.

Cortex.—The anterior third of the skull, including the roof of the orbit, was then removed by first making a trephine opening and subsequently removing the bone piecemeal with fine bone forceps. All bleeding from the bone, which was always free, was immediately checked by wax. In this way the whole of the anterior extremity of the hemisphere, including the orbital surface, was completely exposed, *i.e.*, as far as the margin of the olfactory tract. For the better exposure of the same the tissues filling the orbit were drawn forward, the ocular contents having previously been removed from the eyeball through an incision in the sclerotic.[†] By means of constant irrigation with warm water or normal salt solution shock was in very great measure avoided. This was also provided against in the usual way with hot vessels, coverings, &c.

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[*] Purposely short to allow of proper change of the respiratory gases in ventilation of the lungs.

[†] Or the eyeball removed (HITZIG).

In no case was the dura mater opened until immediately before the commencement of the excitation.

The animal was then fixed on its side so that when the anterior wall of the trachea had been removed a perfect view from below was obtained of the vocal cords in their whole length.

In all this preparation of the trachea, larynx, &c., special care was necessary to avoid injury of the recurrent laryngeal nerves. Between every period of the excitation of the cortex it was douched with warm water or saline solution, protected by the skin-flap from the air and kept warm with hot sponges.

Corona Radiata.—The investigation of the corona radiata of course enables one to decide many points concerning the amount of representation of various functions in the cortex. Naturally, however, the excitation of the few fibres descending from the comparatively extensive area of the cortex is not easy unless the electrodes be placed exactly upon the cut ends of the fibres. It is for this reason, no doubt, that a stronger stimulus* is usually required to successfully excite the fibres. The removal of the cortex was always effected by a single incision with a sharp scalpel at right angles to the supposed direction of the fibres.

Internal Capsule.—This was exposed by horizontal section through the hemisphere in the same way as that just described for the corona radiata. The line of the incision taken is referred to on p. 202, and the only point noteworthy here is the arrest of hæmorrhage, &c. Naturally bleeding comes almost entirely from the middle cerebral, the lenticulo-striate arteries and their branches. Bleeding from these vessels can be certainly arrested if a fragment of amadou be gently pressed on the open mouth of the vessel and left there. Usually the various bundles of fibres in the capsule were then explored with the electrodes, and finally a careful transcript of the surface of the section made with compasses upon paper ruled with squares of 1 mm. a side, and the corresponding bundles of fibres indicated by arbitrary numbers placed on the squares into which the capsule was by this means divided.

The Medulla Oblongata.—This was exposed for excitation by reflecting the muscles and periosteum by the usual T-shaped incision from the occipital bone and the dorsal surfaces of the arches of the first two vertebræ without injury to the vertebral vessels. These same arches and the neighbouring portion of the occipital bone were then cut away with bone forceps. The dura mater was then divided in the middle line and the middle lobe of the cerebellum slightly drawn upwards or a portion removed in order to expose the lower end of the fourth ventricle. A drawing was then made with compasses of the surfaces of the ventricle thus exposed on the 1 mm. ruled paper. Oozing from the cerebellar vessels was always readily controlled, even in the dog, by irrigation with hot water or saline solution. This had a very notable effect also in raising the excitability of the bulbar centres when these were depressed by shock, exposure, &c.

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* PUTNAM, FRANCK.

In every case a post-mortem examination was made, the drawings verified and the specimen preserved.

d. *Influence of the Anæsthetic and Strength of Stimulus.*

We have assumed that the construction of the whole neuro-muscular apparatus of the larynx comprises (1) an area of cortex popularly, though incorrectly, termed the cortical laryngeal centre, (2) a similar area in the bulb or medulla oblongata which may in like manner be spoken of as the bulbar laryngeal centre and is connected with the cortical apparatus by fibres running in the corona radiata and internal capsule, while finally the vago-accessory nerve roots and peripheral branches contain the fibres supplying the laryngeal muscles and mucous membrane.

It was first observed by HOOPER[*] that even when the recurrent nerves were cut inhalation of large doses of ether produced paralysis of the closers (the adductors) of the glottis before the openers (the abductors). We repeated[†] and extended in further detail this observation and showed that this remarkable peripheral and differential action of ether was, in all probability, due to the fact that the antagonistic muscles of the larynx belong to classes of muscles biologically different.

HOOPER'S original observation was contested by DONALDSON,[‡] who found that in certain cases one of the two groups of muscles predominated according to the strength of the stimulus, that with a feeble current, opening, with a strong current, closing, of the glottis was produced. A further, later research by HOOPER[§] showed that the same effect is produced by varying the rate (*i.e.*, the intensity ?) of the stimuli, with a slow rate of interruption of a constant current abduction being obtained, with a quick rate adduction.

We have observed DONALDSON'S result to be occasionally present, and from general considerations are ready to believe that HOOPER'S second observation is correct. It is clear that the ether effect, and the intensity of stimulation effect mutually confirm each other. All these results apply in their entirety to Dogs only. Both, however, have to be kept in view when considering the results of exciting, as in the present research, the highest point of the efferent neuro-muscular track of the laryngeal apparatus in any animal, since it is obvious that the actual representation of movement (whether closure or opening of the glottis) might be masked by the condition of the peripheral mechanism; for instance, if this were poisoned with ether stimulation would give opening only of the glottis.

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[*] 'Transactions of the American Laryngological Association,' vol. 7, 1886.

[†] 'Brit. Med. Journal,' 4–11 September, 1886. *Vide* also BIEDERMANN, 'Centralblatt für Physiologie,' and BOWDITCH, 'International Journal of the Medical Sciences,' April, 1887, p. 444.

[‡] 'American Journal of Medical Sciences,' July, 1886.

[§] 'Transactions of the American Laryngological Association,' 1888.

This combination of physiological relationship in the larynx has not, so far as we know, received much attention, we wish, therefore, to lay stress upon the fact that, until it has been further investigated, we shall not speak dogmatically upon the relative degree of representation of the two antagonistic movements in any one point of the cortex, but shall content ourselves with giving the results of our work. The further consideration naturally arises, that possibly what applies to the peripheral mechanism *may* also be true of the central apparatus, that, in short, the activity of the cortical corpuscles in which the representation of adduction exists may be more easily extinguished by ether than that of the representation of abduction. Considering, too, that this implies the earlier abolition of purposive function, it is not so fallacious to thus translate peripheral (*i.e.*, nerve ending ?) conditions to a centre. This, however, although a question of the utmost interest, does not appear to be capable of direct solution until it is possible to differentiate either anatomically or functionally the particular fibres in the pyramidal tracts in which closure or opening are respectively represented.

We hope that the results of excitation of the internal capsule, especially in the Cat, *vide infra*, will lend some aid in explanation of the difficulty as well as in the special examination of MASINI's results for the reasons before given. We have carefully noted the effect of varying the strength of the excitation.

We have always employed the same rate of excitation (viz., 100 per second), since we believe that variation in rate is practically the same in effect as variation in intensity.

RESULTS.

Cortex.

General Statements.

We have directed our attention primarily to the investigation of the representation of phonatory laryngeal movements only, but we have not been unmindful of the concomitant representation of respiration. This is a point which has already been the subject of research, and especially at the hands of FRANÇOIS FRANCK. That author, as already mentioned in the Historical Retrospect, does not consider that a separate cortical apparatus exists for the phonatory and respiratory functions of the larynx respectively, but we believe that an extensive series of experiments will justify the course we have adopted.

We moreover think it right to discriminate between the representation of general respiration and that of the larynx, since we have, on the one hand, obtained laryngeal effects without any concomitant changes in general respiration,* and on the other hand, one excitation has often at the same moment induced changes of a different type in the larynx and general respiration, *e.g.*, closure of the rima glottidis with general acceleration of respiration. We shall therefore proceed at once to describe the laryngeal effects only, and shall reserve what we may wish to state relating to the effects produced on general respiration for another communication. In arranging our results we divide them as indicated on p. 188, *i.e.*, first, according to the species of animal employed, and we shall commence with the highest order.

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* Since this was written KRAUSE has stated in the 'Berliner Klinische Wochenschrift,' No. 25, 1890, that he has observed the same differentiation of representation.

Monkey.

Species employed.—We have explored the cortex in examples of *Macacus sinicus*, *Macacus rhesus*, and *Macacus cynomolgus*.

Among these *Macacus sinicus* afforded the best results. The general conclusions we derive from our excitation experiments are as follows :—

Intrinsic Laryngeal Movements.—That in the foot of the ascending frontal gyrus, just behind the lower end of the præcentral sulcus (*vide* Plate 31, fig. 1),* there is a focus of representation of the movements of the vocal cords which are independent of movements of the pharynx, when the most anterior part of the focal area of representation is excited.

This focus is limited anteriorly by the præcrucial sulcus (*p.c.*, fig. 1) and a line continuing the direction of that sulcus to the Fissure of SYLVIUS, superiorly, by a line drawn horizontally (parallel to Fissure of SYLVIUS) through the upper extremity of the small secondary sulcus marked *v*, see fig. 1, inferiorly, by the Fissure of SYLVIUS, and posteriorly, by the sulcus *v*.

The purely intrinsic movement of adduction of the vocal cords seems to be represented in the front half (marked darkly F, in fig. 1) of this focal area. In the posterior half, *i.e.*, just in front of *v*, it is accompanied by pharyngeal movements especially. (BEEVOR and HORSLEY.)

In this focal area the character of the movement represented is invariably adduction (Monkey), and not only complete, but also perfectly bilateral. We have never observed abduction to follow excitation. Outside the focal area the intrinsic movements are also represented, but in a greatly diminished fashion. Thus, from the rest of the facial region, as high as the lower border of the upper limb region, as defined by BEEVOR and HORSLEY, and, posteriorly, as far as the secondary sulcus in the foot of the ascending parietal gyrus, a slight degree of adduction (as far as the cadaveric position) is obtained on excitation. The relative degree to which this exists is shown in fig. 1 by the depth of the stippling. It need hardly be added that, of course, the movements of the face, jaws, and tongue noted to be represented in this region (FERRIER, SCHÄFER, BEEVOR and HORSLEY) also occur in concomitant association.

This gradual decrease in representation from a focus or centre of most complete function is typical of all cortical motor representation, especially in the lower apes.

Extrinsic Laryngeal Movements.—The movements of the larynx as a whole, of course, possess considerable interest. From anatomical reasons these resolve themselves under two headings—

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* Confirmed by MOTT and SCHÄFER, 'Brit. Med. Journal,' May 17, 1890.

(1) Upward Movement of the Larynx,
(2) Downward ,, ,, ,,

(1) *Upward movement* of the larynx we noted to occur only in front of the Fissure of ROLANDO, between it and the small secondary sulcus marked v in figure.

This movement is associated with swallowing and mastication, these actions being (BEEVOR and HORSLEY) represented in the strip of cortex thus indicated. Clearly, in this association, we have only the completion of the observed representation of these complicated acts.

(2) *Downward movement* of the larynx we obtained by exciting the cortex just behind the Fissure of ROLANDO between that sulcus and a line parallel to it, drawn from the lower end of the intraparietal sulcus to the Fissure of SYLVIUS.

Once we observed confusion between the movement of the larynx upwards and downwards to occur at this point, the downward direction predominating.

Epilepsy.—We have frequently observed epilepsy to follow excitation of the cortex in this region. At the commencement of the fit, the vocal cords are strongly adducted, often with tremors, *i.e.*, confusion between adduction and respiratory (?) abduction, this persisting during the tonic stage. Then, in the subsequent clonic stage, the movement of adduction alone occurs as single spasms and ceases, of course, often suddenly.

Carnivora.—Dog.

Phonation.—The following account applies only to the adult animal; we shall speak later of the differences which are caused in the cortical representation according to the age of the individual examined. The nomenclature of the sulci employed will be that given by LANGLEY in his admirable paper on this subject,* except that for brevity we shall speak of the anterior limb of the sigmoid gyrus as the præcrucial gyrus, and similarly of the posterior limb as the postcrucial gyrus. In the original description given by KRAUSE† of the cortical representation of the movements of the vocal cords, that author localised the focus of the representation to be situated in the præcrucial gyrus [or, as he called it, following MUNK, the gyrus præfrontalis (OWEN),] just where that gyrus terminates below in a narrow pillar or isthmus connecting it with the anterior composite gyrus. At this point he found that excitation, as a rule, produced bilateral adduction of the cords; this we have completely confirmed, but we have also found that while the spot indicated is a focus, nevertheless slight adduction can be obtained by excitation of the whole of the lower two-thirds of the præcrucial gyrus, and also a few millimetres of the upper extremity of the anterior composite gyrus.

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* 'Journal of Physiology,' December, 1883, p. 248.

† 'Archiv f. Anatomie und Physiologie, Phys. Abth.,' 1884, p. 203.

This representation of the intrinsic movements of the larynx is not pure except very special care be taken to adjust the strength of the excitation sufficiently to prove a minimal stimulus to the point excited. As a rule, it is accompanied by movements of the tongue and of the pharynx, *e.g.*, swallowing.* Occasionally, however, we have obtained movements of the vocal cords without any concomitant action elsewhere. We have never, in the adult Dog, witnessed abduction, although we have explored the whole of the frontal lobe on its orbital and external nasal surfaces completely.

Respiration.—We now proceed to remark upon the representation of respiratory movements of the larynx also to be found in the cortex of the adult Dog. We have found that the following conditions may be produced with absolute certainty.

a. Acceleration of Respiratory Movements of the Vocal Cords.—This is chiefly represented just above the focus for the movements of the adduction of the cords, *i.e.*, just in the middle of the lower third of the præcrucial gyrus, but excitation of the whole of the præcrucial gyrus as a rule produces this effect in diminishing degree, as we move from the focal point just mentioned. In the performance of this act the abduction of the vocal cords is, as a rule, diminished in extent, as has already been mentioned in speaking of their phonatory representation in the same area, but they otherwise present the ordinary alternate rhythm of abduction and adduction.

Before passing to the next point observed we must here make a few remarks upon this extraordinary result, because it has not been, so far as we know, described in connexion with any function other than the respiratory.

Quickening of respiration has very properly been termed by RICHET[†] polypnœa, and has been proved by him to be the means whereby the thermo-taxic apparatus restores the equilibrium of the body by providing for extra loss or dissipation of heat.

Further, work of a memorable kind has been done upon this subject by OTT,[‡] who has directed special attention to this point, and has produced by excitation the same acceleration of respiration, but from excitation of the internal capsule. (*Vide* our remarks on the internal capsule.) We provisionally quite agree with the conclusions and explanations offered by these writers, and we would here remark, that so far as we can see, the results obtained by CHRISTIANI,[§] and probably those by MARTIN and BOOKER,[||] are to be explained as the results of excitation of the fibres leading down from this very extensive and cortical representation of the respiratory acceleration

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[*] [While this paper was passing through the press MUNK published, in the 2nd edition of his 'Gesammelte Mittheilungen über die Functionen der Grosshirnrinde,' a statement on p. 178 to the effect that we have confounded the focal representation of phonation with laryngeal movements when accompanied by associated movements of the mouth, pharynx, &c. The justice of this statement we leave to the opinion of our readers.—August, 1890.]

[†] 'La Chaleur Animale.'

[‡] 'Laboratory Researches,' Easton, Pa.

[§] 'Zur Physiologie des Gehirnes.' Berlin, 1885.

[||] 'Journal of Physiology,' vol. 1, 1881.

that we have observed. (*Vide* also FRANÇOIS FRANCK, LÉPINE, BOCHEFONTAINE, DANILEWSKY, GOLDSTEIN, SIHLER, MUNK, &c., and our remarks on the internal capsule.)

b. Intensification of Respiratory Movements.—If the electrodes be moved over the surface of the sigmoid gyrus it will be noticed that as soon as they are placed opposite the lower or outer end of the crucial sulcus, there is then, together with the now very slight acceleration in rate, a distinctly more energetic action of the vocal cords. Both the abduction and the adduction movements are more pronounced, and as the electrodes are carried back to the lower end of the postcrucial gyrus, *i.e.*, over the area of representation of the fore-limb, this intensification becomes still more marked, and is occasionally accompanied by slowing, and may in short be said to be there localised, as from this point upwards it gradually diminishes over the surface of the gyrus.

These observations are interesting in connexion with those made by MASINI upon the distribution of the laryngeal represention in the Dog. (*Vide* History.)

In reviewing the results just noted, we wish to point out that if the excitation of the cortex be first attempted with an extremely weak current and if then the stimulus be increased, the first effect in response to the weak current is the respiratory acceleration before noted, and the next effect is the intensification of the respiratory movements. The purposive adduction obtained in the phonatory centre as a rule requires the strongest stimulus.

This has been found to be the case by most observers, the distance of the secondary coil from the zero point of the ordinary DU BOIS inductorium being required to be pushed, as KRAUSE himself first stated, to 7·5 or even 4 cm.* Although we have made a special investigation of this point with very weak as well as stronger currents, and although we have been very careful to preserve the vertical position of the larynx, and to record even the slightest action, we have never observed the unilateral movements described by MASINI.

Epilepsy.—As in the Monkey, we have not infrequently observed epilepsy to follow the excitation of the cortex, this being more readily produced in the carnivorous animals than in the higher. During the epileptic convulsions the vocal cords usually after preliminary adduction exhibit clonic adductory movements, in no wise differing from those previously described, save in their intermittent character.

Cat.

We have made a large number of experiments upon the cortex of the Cat because we found very early in our investigations, in 1886, that the movements of the larynx represented in the cortex of the Cat were not the same as those which we had obtained from the Monkey or even from the Dog. In other words: contrary to what we have just seen, the movement of abduction was well represented in the cortex of the Cat, although we had never been able to find any genuine trace of it in the cortex of the Dog. It will be necessary, perhaps, first to explain that the arrangement of the convolutions in the Cat as regards the frontal lobe is in its chief features the same as in the Dog, only in miniature. See Plate 32, figs. 2, 3, 4, 5. The coronal fissure bounds the sigmoid gyrus below, and running forward is separated from the supraorbital sulcus by the pillar or isthmus of the præcrucial gyrus joining the anterior composite gyrus as before described. In front of the supraorbital sulcus and between that sulcus and the rhinal fissure is situated, as in the Dog, the orbital lobe. The rhinal fissure, of course, separates the orbital lobe from the olfactory tract. We mention all these points because their special bearing will be seen directly.

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* Faradism, moreover, not HELMHOLTZ modification.

Phonation.—The bilateral adduction of the vocal cords, as in phonation, we have observed in the Cat to be more frequently represented in the coronal gyrus at its anterior extremity, near the anterior composite gyrus, at a point which is in a line with the crucial sulcus and in the upper part of the gyrus, *i.e.*, close to the coronal fissure, at *d′*, figs. 2, 4, 5. We have further observed that representation of bilateral adduction is also to be found in the area corresponding to that discovered by KRAUSE in the Dog, *i.e.*, just above and in front of the anterior end of the coronal fissure, at *d*, figs. 2, 4, 5. This representation of adduction, whether in one place or the other, is very soon exhausted, although it is, when present—*i.e.*, in a full-grown old Cat—well marked. It requires a moderate stimulus for its production, *i.e.*, 7000 to 8000 of the KRONECKER coil.

Respiration, Abduction, Acceleration.—We have found that in the Cat there exists a point (at *b*, figs. 2, 3, 4, 5) in the lower border of the hemisphere, just above the rhinal fissure—*i.e.*, in the anterior composite gyrus—and just below the depression representing the antero-supra-sylvian sulcus, excitation of which produces well-marked—*i.e.*, as long as the excitation lasts—abduction of the vocal cords; and that the same effect is produced, in a diminishing degree, round this point as a focus, and occasionally passes above the supra-sylvian sulcus on to the coronal and upper part of the anterior composite gyrus. This cortical representation of abduction in the Cat is very interesting, as probably indicating special respiratory requirements* in that animal, this deduction being confirmed by the experiments of LEGALLOIS† and others. Although we have found occasionally that in the Cat the præcrucial gyrus gave upon excitation, as in the Dog, acceleration of respiration, yet this was not so marked.

Intensification.—Similarly, intensification also was observed, but in no great degree.

Concomitant Movements.—Concomitant movements were observed (movements of the tongue, licking, mastication, and swallowing) when the anterior composite gyrus was excited, *i.e.*, when opening of the glottis (abduction) was produced. But we constantly observed the abduction to be completely maintained while thoracic respiration went on unhindered. On the other hand, when closure of the glottis was evoked, the respirations were distinctly slowed.

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* In the discussion following a demonstration of some of our experiments at the 10th International Medical Congress, 1890, Prof. DU BOIS-REYMOND stated that he had observed phonation in the Cat and Cow to be of an inspiratory nature. Prof. EXNER stated the same with regard to the Pig.

† 'Sur le Principe de la Vie.'

We cannot pass from this part of the subject without adverting to the remarkable way in which the laryngeal apparatus of the Cat is, as we have before remarked, extremely sensitive to the operation of the anæsthetic. Especially was this the case in making these experiments upon the cortex, since we found that a moderately deep narcotisation was sufficient to change the effect observed from adduction to abduction. The discussion of this we resume further on.

Epilepsy.—We have occasionally observed epilepsy, and when it occurred the vocal cords were preliminarily brought together, and then moved in clonic adductory spasms. We would now like to state that it is the phonatory—or, as we may say, the purposive—adductory representation of the laryngeal movements which is invariably brought out in the epileptic discharge of the cortex; another proof, if proof be required, of our position that adduction is a movement characteristic of the highest cortical evolution as far as the larynx is concerned.

Rodents.—Rabbit.

Cortical representation of movement in the Rabbit is, of course, well known to be very limited indeed, both in extent and in degree, the cortical centres being soon exhausted and the effects produced being relatively insignificant. We therefore only made two experiments upon this animal. We obtained no focal representation of the larynx, but the intrinsic movement observed concurrently with the movements of other parts were, as a rule, adduction; and, where this was most marked, the concomitant movement was that of swallowing.

Corona radiata.

We have, in a certain number of experiments, removed the cortex and excited the fibres beneath. As might be expected, our results all point to one conclusion, viz., that excitation of the fibres which lead in a direct line from the particular part of the cortex removed to the internal capsule gives the same effects as did the cortex when that was excited. Thus, in the Dog we have observed that the white fibres leading down from the præcrucial gyrus gave acceleration and those from the isthmus of that gyrus adduction, whereas the fibres coming from the lower end of the postcrucial gyrus gave intensification of the respiratory movements of the vocal cords. Exactly the same is observed in the Cat, viz., that acceleration is coupled with adduction, and that, on excitation of the fibres coming from the abductor focus, we have as distinctly abduction.

In no case, in accordance with the previous observations of various authors, did we obtain epileptic movements of the laryngeal muscles, after the cortex had been excised, by stimulation of the fibres leading therefrom.

Internal Capsule.

It will be necessary to give a slight anatomical introduction before describing our results of the excitation of the internal capsule. In the first place we invariably have exposed the internal capsule by a horizontal section carried through the substance of the hemisphere from before back, after the usual preliminary ligature of the middle cerebral artery. In this manner the internal capsule in its whole length, basal ganglia, &c., were exposed, and readily distinguishable. The horizontal section before referred to passed in the Carnivora through the sub-prorean gyrus, the lower part of the orbital lobule just above the rhinal fissure, through about the middle of the Sylvian fissure, and so backwards through the lower end of the curved external convolutions and sulci, *i.e.*, ecto-sylvian, &c.

In the Monkey the section was carried horizontally backwards through the third frontal gyrus, the foot of the ascending frontal and parietal gyri respectively, across the Sylvian fissure, through the uppermost part of the temporo-sphenoidal lobe, and so through the occipital lobe. The anatomical features of the cerebral sections thus produced, although, of course, differing considerably in the various orders of animals, nevertheless are not so diverse as might be anticipated (see figs. 6, 7). In each case the section exposed both the caudate and lenticular nuclei of the corpus striatum as well as the optic thalamus. The sections in the Monkey thus correspond to about the level of Group 4, as described by BEEVOR and HORSLEY. These authors in their paper (*ante*, pp. 49–88), on the arrangement of the excitable fibres of the internal capsule of the Bonnet Monkey, just referred to, observed phonation to occur in one section of the capsule when these fibres were excited (*ibid.*, p. 83), but they did not directly observe the laryngeal movements.

In this connection it must be remarked that in the Carnivora the lenticular nucleus is relatively extremely narrow (see figs. 6, 7), so that the angle made by the two limbs of the capsule is a very open one, almost 150 to 160 degrees. Therefore, as will be seen directly, the general arrangement of the fibres, as far as the antero-posterior order goes, is the same in the two classes of animals, although the actual positions are not quite the same, owing to the non-development of the præfrontal region in the Carnivora. Since the irruption of præfrontal fibres which makes up the mass of the anterior limb in the Monkey and pushes the excitable fibres further backwards into the posterior limb does not occur in the brain of the Dog or Cat, in these animals it is the anterior limb which principally contains the excitable laryngeal fibres.

In all animals the most anteriorly placed laryngeal effect observed was the accelerated movements of the vocal cords connected with quick movements of the thorax in the polypnœa, which we have described to be produced by excitation of the præcrucial gyrus. In the Cat and in the Dog this acceleration of respiration is produced by excitation of a considerable number of fibres occupying the anterior half of the anterior limb, *i.e.*, opposite about the anterior half of the caudate nucleus as exposed in the section before referred to. At the same time that acceleration was produced there was also obtained from the most posterior bundles of these fibres, in all animals, abduction, this combination being concentrated in the Monkey at the genu, where the fibres subserving the acceleration of respiration are chiefly grouped. In the Cat and in the Dog these abductor fibres were found just before the genu.

Taking the various species individually we find that, in (1) the Monkey, acceleration is first produced when the fibres immediately in front of the genu and exactly at the genu are stimulated; this is, of course, just opposite the sharp angle made by the middle zone of the lenticular nucleus. The fibres in the posterior limb immediately behind the genu when excited either give a mixed movement or simply produce on excitation diminution of abduction, and it is not until we get to the junction of the middle and posterior fourths of the capsular border of the middle zone of the lenticular nucleus that we get distinct adduction. There, however, the adduction is very accurately localised to a few bundles of fibres about 2 square millimetres in area. Just behind this point for a short distance diminished abduction was observed on stimulating the capsule in one case; it is clear, therefore, that in the Monkey the acceleration of respiration is only brought about by a few fibres at the situation of the genu, while the phonatory adduction of the cords is subserved by a few fibres in almost exactly the middle of the posterior limb of the capsule.

It may be interesting at this point to state that this is what might have been expected, inasmuch as it is just at this region that the observations before referred to* show that these fibres similarly subserve the movements of the tongue and pharynx.

(2). In the Dog the condition appears to prevail which is found in the Cat, about to be described, that is to say, that excitation of almost the whole of the anterior limb produces acceleration of respiration and that adduction begins to be produced at the genu. (*g*, fig. 7.) We will therefore proceed to describe the condition as it is seen in the Cat, in which animal we have investigated this point closely.

(3). In the Cat the most anterior effect is acceleration. This commences, according to the level of the section, either just in front of, or just opposite to, the anterior extremity of the caudate nucleus, and it persists throughout the front half of the anterior limb of the capsule. (1–3, fig 6.) At this centre point of the anterior limb the respirations become intensified, abduction much more notably marked, and in some cases persistent. (See fig. 6.)

Exactly at the genu, or in many cases just in front of it, *i.e.*, opposite the posterior extremity of the caudate nucleus (*vide* figs. 6 and 7), adduction is very sharply marked.

In most cases the bundle of fibres subserving this phonatory adducton is small, in others—possibly owing to slight difference in the obliquity of the section—

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* Beevor and Horsley, *loc. cit.*

adduction can be obtained from almost any point in the front half of the posterior limb, and in some cases there is, in addition, diminished abduction as far as the hinder end of the lenticular nucleus.

We are now in a position to discuss further the points postponed in speaking of the relative representation of respiration and phonation in the cortex.

It will be seen that in the capsule we have thus arranged antero-posteriorly the fibres subserving portions of the cortex which are placed rather transversely to the mesial plane than parallel to it, and that, as might be expected, the acceleration which is the highest and most anterior is similarly most anteriorly placed in the internal capsule. To return now to the polypnœa obtained by exciting these fibres in the internal capsule, OTT describes how by using needle electrodes he was enabled in the Rabbit and in the Cat to evoke exactly the same polypnœic condition that we produced in the above-mentioned circumstances. He was exciting the fibres, according to our view, of the capsule leading from the cortex. The very important results which he obtained, and the bearing which these facts have upon heat regulation and the pathology of fever will be found in his communication.

The next point is of course the relation which the laryngeal movements thus described bear to the other respiratory movements. Where we had to do simply with the acceleration of the laryngeal movements, of course such acceleration was exactly synchronous with acceleration of thoracic respiratory excursions.

But when the fibres posterior to this were excited, viz., those which produced persistent abductory movements of the vocal cords, then it was noticed that while the larynx remained wide open in persistent abduction as long as the excitation lasted, nevertheless the respiratory excursions of the thorax were greatly accelerated; another instance of the differentiation of representation which we have before described. Next, when the vocal cords were brought together in adduction, as a rule there was some slowing of respiration and frequently movements of the opposite fore limb and swallowing.

Epilepsy.—After what has gone before it will be easily understood that we never saw epilepsy to occur from excitation of the internal capsule, and that all intrinsic laryngeal movements observed were strictly and completely bilateral.

Medulla oblongata.

We come now to the consideration of the laryngeal movements produced by direct excitation of the medulla oblongata. It will readily be conceded that here there is more than usual difficulty in discriminating between those laryngeal movements which subserve the process of respiration and those which have to do with phonation. We do not propose in the present case to do more than indicate what those movements are, and to leave the consideration of the shares which they individually possess in serving the two functions before mentioned to another time.

But we may observe incidentally that we are naturally inclined to regard that small area of the medulla from which adduction can be produced as a transit-station for the corresponding cortical, and as a centre for reflex phonatory impulses. Whether this is really so the future will show. What is, for the present, of more practical import in this connection is how far the bulbar apparatus for the larynx is bilateral or unilateral in its composition. It will be seen directly that we have obtained from the one half of the medulla oblongata both bilateral and unilateral effects, that is, as far as they go the bilateral effect is for the most part complete, sometimes, *i.e.*, when the electrodes are moved outwards, with a preponderance of movements on the part of the cord on the same side, and the unilateral effect is of course movement of the cord on the same side as that stimulated.

We shall discuss the results then from these two standpoints, viz., (1) the bilateral effect, and (2) the unilateral effect.

We have only made observations on the Carnivora, and in this respect it is interesting and important to note that the results in the Cat are not different from those in the Dog. In fig. 9 is given a photograph of the floor of the fourth ventricle in the Dog, the calamus scriptorius (*c.s.*, fig. 9) is well seen bounded laterally by the fasciculus gracilis passing up on each side towards the restiform body with the ala cinerea (*a.c.*, fig. 9) well marked. The cerebellum has been divided and the right half removed, so as to expose the lower surface of the inferior peduncle completely, and only the upper part of the inferior vermiform process is seen to be in contact with the floor of the ventricle.

Within the area thus exposed are included all the movements of the vocal cords which may be reasonably attributed to phonation, and also almost all which are connected with respiration. However, in accordance with what we have stated above, we shall now proceed to describe the movements of the vocal cords independently of the function they may be supposed to subserve.

1. *Adduction.*—Closure of the glottis is sharply and invariably produced when the upper margin of the calamus scriptorius, *i.e.*, the nucleus of the spinal accessory nerve, is stimulated, and the same thing is observed if the electrodes are carried outwards and upwards along the margin of the posterior pyramid for about 3 mm. from the middle line. This action is distinctly bilateral.

Immediately above the calamus, in the situation of the ala cinerea, abduction is invariably produced. This movement, like that of adduction, is also absolutely bilateral and persistent. It extends upwards as high as the line drawn horizontally across the fourth ventricle at the transverse level of the upper end of the representation of the adduction. (See fig. 9.) Above this point, especially in the middle line as high as the level of the eighth nerve, excitation evokes movements of the cords about the cadaveric position (see dotted area, fig. 9), which may be looked upon as either a confusion or imperfect adduction. This movement is strictly bilateral.

We have obtained unilateral adduction of the vocal cord on the same side by excitation of the restiform body in a vertical direction beginning below, opposite and close to the upper end of the region just referred to as giving bilateral adduction, and proceeding along the outer part of the floor of the fourth ventricle as high as the centre of that cavity. (See fig. 9.)

Whether the adduction of the vocal cord of the same side obtained by excitation in the line thus drawn is due to excitation of the nucleus reserved for the movements of the vocal cord of the same side, or whether it is rather excitation of those fibres which run through the substance of the medulla, to appear at once as the roots of the vago-accessory nerves, remains doubtful, though we are naturally more inclined towards the latter view. However, we do not consider that any positive opinion can at present be expressed upon this point.

Abduction.—It has been mentioned above that the movement of abduction is obtained over the situation of the upper two-thirds of the ala cinerea and also from about the origin of the eighth nerve. This latter area is evidently more important and extends upwards to close to the debouchment of the aqueduct of SYLVIUS. (See fig. 9.) Further, this movement of abduction is persistent, and is better marked a short distance, about 2 mm. from the middle line, than in the middle line itself. We have never observed unilateral abduction similar to the unilateral adduction before mentioned.

It may be that fibres exist in the tegmentum or crusta which directly connect together the cortical and bulbar mechanisms now described, and that, as before suggested, the observations which would point to respiratory mechanisms existing in the basal parts of the cerebral hemisphere and in the mesencephalon have been the results of stimulation of such fibres by those looking for respiratory centres in these positions.

Before we had recognised completely the degree to which the etherisation must be carried we obtained some results upon the larynx when the dorsal surface of the spinal cord, *i.e.*, below the calamus scriptorius, was stimulated, but we saw from the first that the results obtained here were probably those of a reflex nature, and further investigation has confirmed this opinion. For the effects were only produced in their entirety as the excitation approached successively the posterior roots, and diminished as the electrodes were moved to intermediate parts of the spinal cord. Further, the effects were far more in the nature of acceleration of thoracic respiration than primary changes in the movements of the larynx.

We never observed any after effects, *e.g.*, clonus, &c., upon cessation of the stimulation of the medulla oblongata.

Influence of Age.

Those acquainted with the history of previous research on the subject of the innervation of the larynx know well that, from the first, experimental investigation has shown that there exists, according to the age, a great difference in the same species of animal in the representation in the nervous system of respiration and phonation respectively.

The need for efficient respiratory action on the part both of the larynx and the thorax is much greater in the younger animal than in the adult, and is greater, as LEGALLOIS more especially has shown, in the Cat and the Horse than in any other animal, especially more than in the Dog. The present part of our paper will be devoted to summarising the facts that we have observed and the differences noted according to the age of the animal, and we shall group the results, as before, according to the species, beginning again with the highest.

(*a.*) *Monkey.*—In the Monkey we have only incomplete observations owing to the difficulty of obtaining many Monkeys, but all our observations went to show that phonatory adduction was less represented in the young animal than in the older adult.

(*b.*) *Dog.*—In the Dog these differences are also marked. In the young Dog even with strong currents we have frequently only obtained from the focus of laryngeal phonatory representation a high degree of acceleration of respiration with marked diminution of abduction, but no complete adduction ; in fact in the cortex of such an animal, while respiration is most efficiently represented, phonation is only imperfectly evolved.

(*c.*) *Cat.*—In the Cat, again, the same thing prevails in its entirety, with the additional point, viz., that this want of differentiation in the laryngeal movements was not confined to the larynx, but also prevailed in the centres for the movements of the limbs.

It is in accordance with points noticed by one of us (V. H.) in the representation of the limb-muscles in the cortex of the Monkey that a wider extent of cortex provides for a higher evolution or development of the motor representation, and probably the differences we have just been describing as produced by age are due to the greater or less provision of cortical material for subserving the particular function represented.

CONCLUSIONS.

The conclusions which we feel may legitimately be drawn from the foregoing experiments—and which, we may be permitted to add, are based not only upon the results of the work just described, but also upon much which we have not alluded to, and which will be described in subsequent communications—may best be put forward upon the plan according to which we believe the central innervation of the laryngeal movements is arranged.

In consequence of the laryngeal muscles serving, as particularly insisted upon by one of us (F.S.), in this connection, two distinct functions (1) phonation, (2) respiration, and in consequence of these two functions being, one connected with so-called purposive or volitionary acts, the other, on the contrary, related to those functions which are commonly spoken of as belonging to organic life, it is easy to understand that our results bring us to the conclusion that the phonatory movements of the laryngeal muscles, *i.e.*, adduction, &c., are represented principally in the cortex, whereas the respiratory movements, *i.e.*, abduction, chiefly in inspiration, adduction less commonly and imperfectly in expiration, usually find their origin in impulses emanating from the bulb.

We have seen that the first of these functions, phonatory adduction, is represented most completely in the cortex the higher we ascend in the animal scale, and the more completely as the cortex is developed in the life of the individual, *i.e.*, by age, while *pari passu*, the function of respiration, although present in a minor degree, as evidenced by acceleration, is least represented where phonation is most completely developed. In further detail, adductory phonation is centred in the Monkey at the junction of the foot of the ascending frontal gyrus, and the base of the third frontal gyrus, in the Carnivora at the junction of the præcrucial, or præfrontal gyrus, with the anterior composite and coronal gyri. Respiration is represented in the higher animals only as acceleration, and that above and rather in front of the focus of phonation.

In the Cat only have we found a deliberate representation of abduction in the cortex.

Turning now to the lowest part of the central apparatus, the bulb, we see that there is therein situated a small but concentrated focus on each side of the middle line for bilateral closure of the glottis, and outside that a small area, excitation of which produces unilateral adduction of the vocal cord on the same side. Above this region of adduction there is also a representation of abduction, *i.e.*, inspiration.

Finally we have found that, connecting the cortical apparatus with the bulbar apparatus, there exist numerous connecting fibres which can be analysed as they pass down from the cortex through the corona radiata and internal capsule towards the bulb; that as far as they are concerned they simply subserve the functions which are proved to exist in the cortex; that the anatomico-functional arrangement of these fibres in the capsule enumerated from before backwards is :—acceleration of respiration, abduction, intensification, adduction; and that their respective positions in the capsule are constant and strictly homologous in the different species of animals, according to the development of the cerebral hemispheres in the particular cases observed.

These results are in complete concord with the ideas concerning the whole central nervous mechanism which innervates the larynx, ideas which were put forward by one of us (F.S.) at the International Congress at Copenhagen in 1884. We are enabled to state this the more positively for the reason that we have in our hands the notes of a large number of ablation experiments which, by their control of excitation effects, prove to demonstration the correctness of the views and opinions we have enunciated.

Description of Plates.

PLATE 31.

Fig. 1. Photograph of right hemisphere of a Macacque's brain, *Macacus sinicus*.

The total or absolute representation of the larynx is indicated by dotting, the depth of the same showing the degree of representation.

R. Fissure of Rolando.
Pc. Præcentral sulcus.
F. Focus of highest development of laryngeal representation, *i.e.*, pure intrinsic movement of adduction.
v. The small secondary sulcus indicated by that letter.
Sy. Fissure of Sylvius.

PLATE 32.

Fig. 2. Three-quarters view of Cat's brain, half natural size.

c.s. Crucial sulcus.
d. Krause's centre of adduction.
d'. Centre of adduction also noted by the authors.
b. Focus of abduction.

Fig. 3. Base of Cat's brain, half natural size
Fig. 4. Side view of Cat's brain, natural size
Fig. 5. ,, ,, half natural size
Lettering as above, fig. 2.

Fig. 6. View of Cat's brain from above. The right hemisphere has been sliced horizontally, as described in the text, to show the internal capsule.

olf. Olfactory lobe.
p.f. Præfrontal fibres.
Ca. Caudate nucleus.
g. Genu.
o.th. Optic thalamus.
n.l. Lenticular nucleus (putamen).
F.S. Fissure of Sylvius.
1. Anterior limit of fibres excitation of which produces acceleration of respiration.
2. Posterior limit of fibres representing acceleration and abduction and commencement of representation of adduction.
3. Centre of anterior limb marking commencement of representation of abduction.

Fig. 7. Horizontal section of the right hemisphere of the Dog. Lettering as in fig. 6.

Fig. 8. View of the bulb of a Cat, the cerebellum being split and drawn aside.

C.q. Corpus quadrigeminum.
cb.p. Posterior ditto and superior cerebellar peduncle.
r. Restiform body.
a.c. Ala cinerea.
c.s. Calamus scriptorius.

Fig. 9. View of the bulb of a Dog, the cerebellum having been split and the right half removed.

aq. Aqueduct of SYLVIUS.
i.v.p. Inferior vermiform process.
a c., *c.s.* As above.

The close oblique markings at the calamus and extending outwards indicate the focus of bilateral adduction.

The vertical lines indicate the representation of bilateral abduction.

The horizontal marks on the outer side indicate the area of unilateral adduction.

The dotted area indicates the representation of incomplete adduction.

All are photographs of the parts in the recent state.

PARALYS…
PRESENTED TO
QUEEN SQUARE, BLOOMSBURY, LON…
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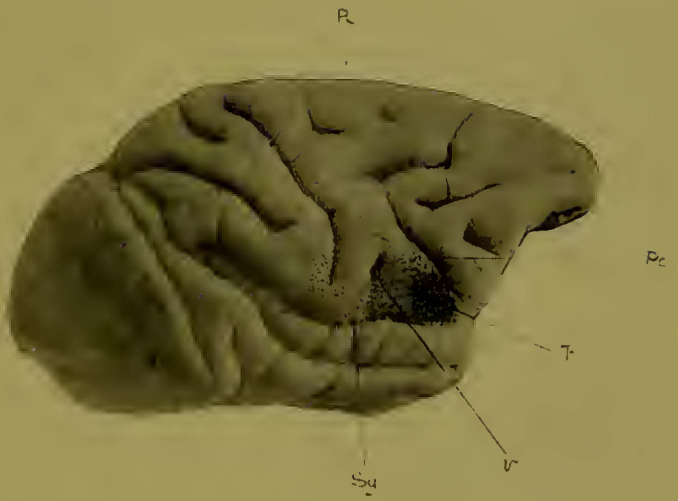

Fig. 1

B Fleming Hanwell

Photo Print.

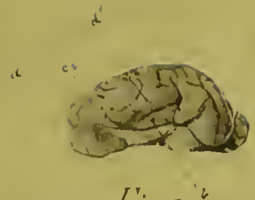

Fig. 2

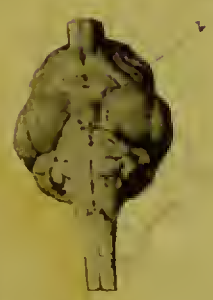

Fig. 3

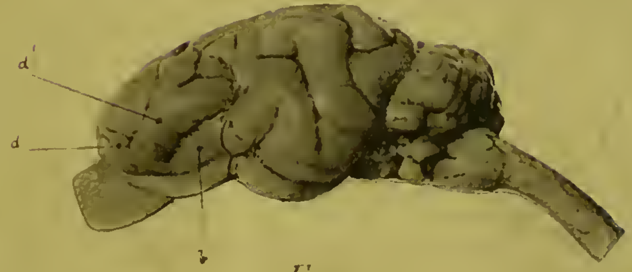

Fig. 4

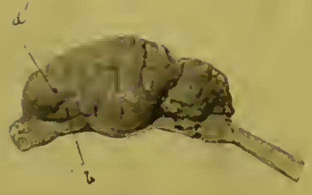

Fig. 5

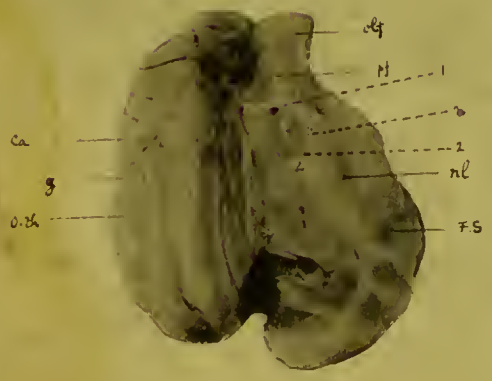

Fig. 6

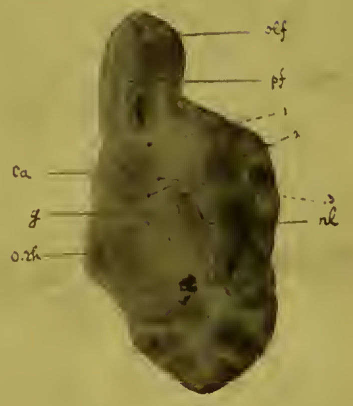

Fig. 7

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QUEEN SQUARE, BLOOMSBURY
PRESENTED TO

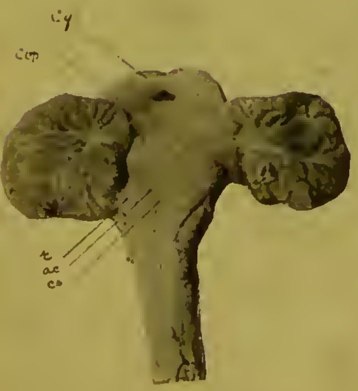

Fig. 8

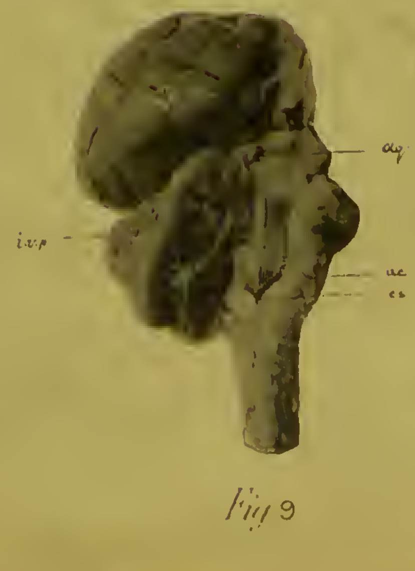

Fig. 9

Photo. Print